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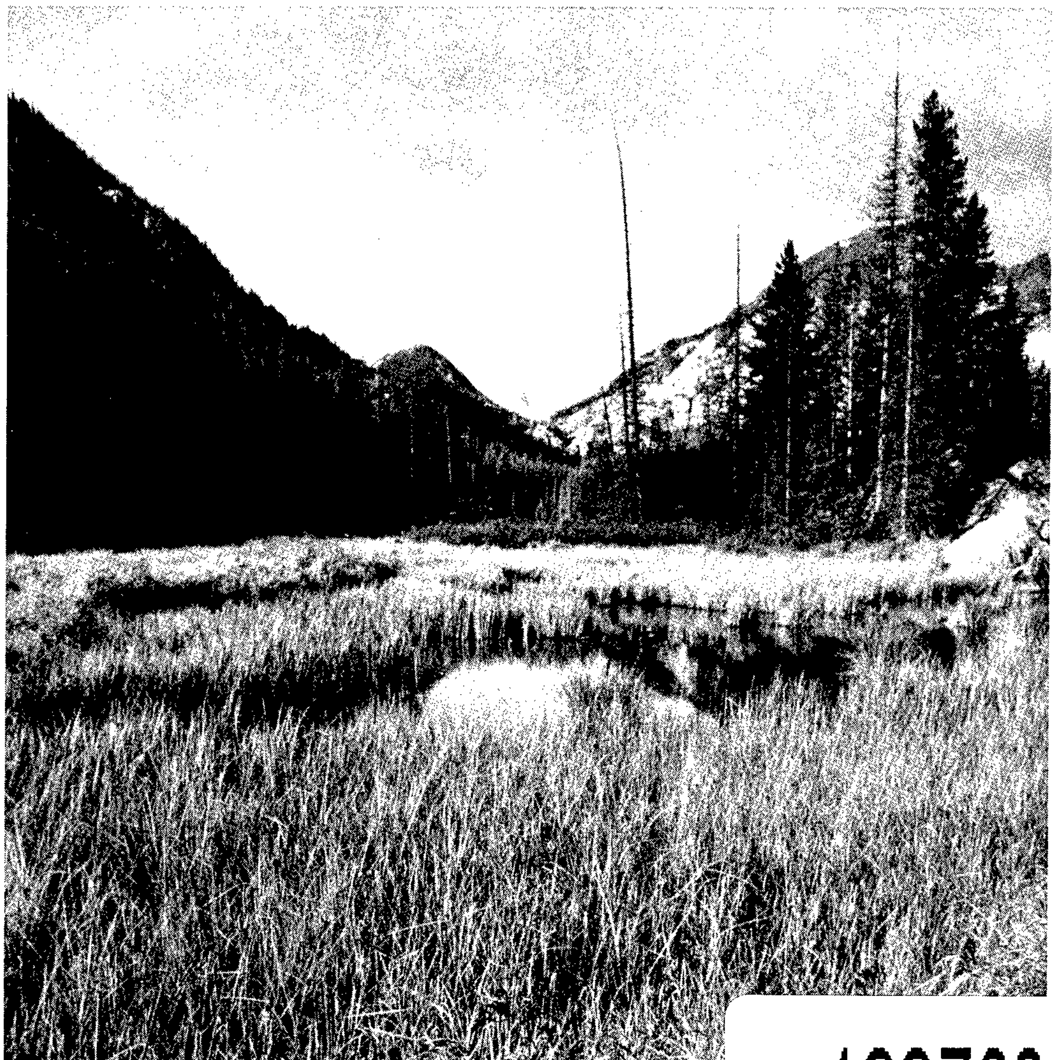
AN ECOLOGICAL CHARACTERIZATION OF ROCKY MOUNTAIN MONTANE AND SUBALPINE WETLANDS



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PREFACE

Material for this ecological characterization was gathered from a wide range of published papers, as well as unpublished reports, other "gray" literature, and the field experience and observations of the authors and editors. An exhaustive literature search revealed a dearth of Rocky Mountain wetland-related articles in scientific journals. Some of the information, especially about ecological processes operating in wetlands, is an extrapolation of other wetland literature. There was no opportunity for any additional field research to be made within the time available for this report. Unless otherwise stated, unpublished data, interpretations, and conclusions are solely those of the authors and editors.

A four-step approach for gathering and reviewing the literature was followed in order to draw on the experience and expertise of wetland researchers, Rocky Mountain ecologists, biologists, and land managers. One hundred fifty-one letters were mailed to persons identified as having interest and knowledge of Rocky Mountain wetlands. Each was requested to recommend their own publications and other works, as well as those by colleagues and others in and outside of their institutions, which they considered important and having information relevant to Rocky Mountain wetlands. Sixty-three responses were received for a 41% response rate.

The first step involved producing a literature search and review of 445 citations. The second step involved tracing references cited in the publications and literature review identified in step one. As copies of literature were collected, they were reviewed for additional publications that were referenced frequently. Step three unearthed additional valuable information, which included analyses of government documents, reports, environmental impact statements, symposium proceedings, management plans, and resource analyses. The fourth step included assembling this information into the seven chapters of this volume.

At the outset, the authors met periodically to share findings and to discuss concepts and approaches to the tasks ahead. Then followed the intensive data assembling and drafting the chapters. These were edited, submitted to the project director for reproduction and sent to a team of nine peer reviewers representing the various fields covered in the report (peer reviewers are identified in the Acknowledgments section). Much additional information was gleaned from a 2-day peer review.

Finally, the authors revised their sections in light of the comments made by the reviewers and the chapters were reedited and coordinated to eliminate duplication and produce a cohesive report.

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CHAPTER 1

INTRODUCTION TO ROCKY MOUNTAIN WETLANDS[1]

1.1 PURPOSE AND GOALS

This document has been prepared to provide a comprehensive review of Rocky Mountain wetlands. It draws on all types and sources of scientific information and is both an analysis and synthesis. We recognized from the outset that large gaps exist in the scientific literature on Rocky Mountain wetlands. An attempt has been made to identify and delineate these gaps in order to estimate the magnitude of research needed to narrow them. Therefore, this document is both a state-of-the-art and state-of-the-science of Rocky Mountain wetlands as of December 1985. This report is intended to provide information for the assessment, planning, and permitting activities of Federal and State agencies. It is also an educational source document for anyone interested in the ecological functioning and value of high-elevation wetlands.

1.2 WETLAND DEFINITIONS

Cowardin et al. (1979) point out that no single, correct definition for wetlands exists, primarily because of a nearly unlimited variation in hydrology, soil, and vegetational types, and because wetlands are lands transitional between aquatic and terrestrial systems. In many cases, wetlands have been described in terms of what they are not. They should not be viewed as dry land, although they may not always be flooded or wet. They are part of a continuous landscape that grades from wet to dry. In many cases, it is not easy to determine precisely where they begin and where they end.

The term "wetland" is a general catch-all to include landscape units such as marshes, swamps, bogs, fens, and lowlands covered with shallow and sometimes ephemeral or intermittent waters. The term also includes wet meadows, potholes, sloughs, the riparian zone, and river-overflow areas. Shallow lakes and ponds, usually with emergent vegetation as a conspicuous feature, are included in the wetland definition, but permanent waters, greater than 2 m (6.6 ft) deep, of lakes and reservoirs, are not included.

U.S. Fish and Wildlife Service Definition of Wetlands

For purposes of the National Wetlands Inventory and the need to develop an acceptable classification system adaptable to all of the Nation's wetlands, the U.S. Fish and Wildlife Service (USFWS) defines wetlands as follows:

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> Wetlands are transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land is covered by shallow water. For purposes of this classification, wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained hydric soil; and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year (Cowardin et al. 1979).

The intent of this definition is to be a reasonable compromise for the many proposed definitions and wetland concepts. It is slightly complex because of the inclusion of technical terms such as hydrophyte and hydric soils. A hydrophyte is defined as any plant growing in water or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content. Common wetland-adapted plants are willows (*Salix* spp.), sedges (*Carex* spp.), rushes (*Juncus* spp.), alders (*Alnus* spp.), and river and bog birches (*Betula fontinalis* and *B. glandulosa*). Hydric soil is defined as soil that is wet long enough to periodically produce anaerobic conditions (i.e., absence of oxygen), thereby influencing the growth of plants.

Wetlands, as defined by the USFWS, include lands that are currently under cultivation (Cowardin et al. 1979), i.e., wetlands on farmlands are not necessarily excluded. Many areas defined as wetlands are farmed during dry periods, but if they are not tilled, cultivated, planted to crops, or heavily grazed or hayed during dry periods (practices that destroy the natural vegetation), the land will support hydrophytes and revert to wetlands (Cowardin et al. 1979).

The dry land, or upland, limit to a wetland is designated as: (1) the boundary between land with predominantly mesophytic (moderately moist) or xerophytic (dry) vegetational cover and land with predominantly hydrophytic (wet, waterlogged) vegetational cover; (2) the boundary between soil that is predominantly nonhydric and soil that is predominantly hydric; or (3) in the case of wetlands without vegetation or soil, such as a pond or stream, the boundary between land that is flooded or saturated at some time each year and land that is not.

Current practice distinguishes between wetlands and deepwater habitats. Deepwater habitats are permanently flooded areas, or lands lying below the deepwater boundary of wetlands. The dividing boundary between inland wetlands and deepwater habitat has been set by Cowardin et al. (1979) at 2 m (6.6 ft).

Legal Definition of Wetlands

Legally, the most widely used definition for wetland is that published in the Clean Water Act of 1972 (P.L. 92-500):

> Those areas that are inundated or saturated by surface or groundwater at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions. Wetlands generally include swamps, marshes, bogs, and similar areas.

This definition is augmented by the guidelines of the U.S. Army Corps of Engineers (COE) and Environmental Protection Agency (EPA), published in the Federal Register.

Riparian Wetland Definition

The term riparian wetland is commonly used to describe certain wetland types, especially in the western United States, including the Rocky Mountains. The term "riparian" is the Anglicized form of the Latin word *riparius* meaning of or adjacent to a river.

The following definition of riparian ecosystem has received widespread support (American Fisheries Society 1980).

> Riparian ecosystems are wetland ecosystems which have a high water table because of proximity to an aquatic ecosystem or subsurface water. Riparian ecosystems usually occur as transitional zones, or ecotones, between aquatic and terrestrial (upland) ecosystems, but they have distinct vegetation and soil characteristics. Aridity, topographic relief, and presence of depositional soils most strongly influence the extent of high water tables and associated riparian ecosystems. Riparian ecosystems are most commonly recognized by bottomland, floodplain and streambank vegetation in the West. Riparian ecosystems are uniquely characterized by the combination of high species diversity, high species densities, and high productivity. Continuous interactions occur between riparian, aquatic, and adjacent terrestrial ecosystems through exchanges of energy, nutrients, and species.

Although most streamside habitat areas are considered riparian, some are not, and may be called nonriparian wetland streamside habitat (Platts 1979). Examples of nonriparian streamside habitat are those areas where sagebrush (*Artemisia* spp.) or other nonhydric community types reach the water's edge, where the streamside habitat is composed of bedrock, where streams are bordered by steep-sided canyon lands, or where streamside environments are composed of boulder and rubble that extends to the terrestrial zone.

There is general agreement that riparian wetland ecosystems tend to parallel the linear and branching configuration of stream channels. For analytical purposes, the riparian wetland may be considered as a component part of the much larger drainage, catchment, or watershed system and thereby becomes a functional part within the larger watershed ecosystem concept (Odum 1971).

Ecologists have long recognized the watershed as the basic unit of study at the ecosystem level, the role of geomorphology in ecosystem functioning, and the importance of the terrestrial-riparian-wetland-aquatic linkage. The river continuum concept (RCC) (Vannote et al. 1980) represents a synthesis of these ideas and proposes that natural stream ecosystems may be characterized as extending from their headwater beginnings (i.e., first order tributaries) to their mouth, and thereby provide a continuous gradient of physical conditions that affect organic matter storage and transport and the response

of biotic communities. There is an overall tendency for the physical conditions to change progressively and predictably with increasing stream size. Thus, a coalescing network of streams within a drainage basin represents a longitudinally linked gradient of physical habitat conditions that support a continuum of biotic communities and ecosystem material processes.

We propose that riparian wetlands form an essential functional role within the RCC, and that these wetlands provide a continuous gradient of physical, biological, and chemical conditions that change progressively and predictably with increasing stream size, elevation, temperature, and growing season.

In most of the western United States, riparian wetland ecosystems may occur within sharply defined community types of moderately moist (mesic) vegetation within the much drier (xeric) surrounding areas, and are often referred to as "gallery forest" or "bosque" (i.e., a small wooded area, thicket, or grove), streambank riparian, lakeside, or pondside vegetation.

The term riparian wetland is also applied to other community types of Rocky Mountain vegetation, such as those associated with dry lakes (playas), springs, arroyos, washes (a dry gulley with ephemeral stream), and Northern Plains draws (gulleys or ravines that water drains into or through at times), by some authorities (Boldt et al. 1978; Johnson and Carothers 1980). In each case, these diverse habitat types (riparian habitat, gallery forest, bosque, playas, arroyos, springs, washes, and draws), though seeming to be dry land most of the time, are considered riparian wetlands based upon the prevalent vegetation (wetland adapted), hydrology (annual inundation or high water table), and soil (hydric) characteristics.

Other definitions consider riparian habitat to be a specialized form of wetland where streambank terrestrial soils are periodically inundated, or frequently subjected to waterlogging, but not necessarily submerged for part of each year (Brown et al. 1978; USDI-BLM 1979a).

1.3 PHYSIOGRAPHIC SETTING

The Rocky Mountains, as a physiographic unit, extend from northern Mexico through Canada and the Brooks Range of Alaska to Point Hope on the Chukchi Sea south of Point Barrow, Alaska. However, this ecological characterization encompasses only the area from the Mexico-United States border in New Mexico north to the Canada-United States border in northern Montana and Idaho (Figure 1). By extending south into the Pecos Highlands and other southern New Mexico ranges, the characterization includes "islands" of Rocky Mountain-type landscape, which support wetlands similar to those of the Rocky Mountains.

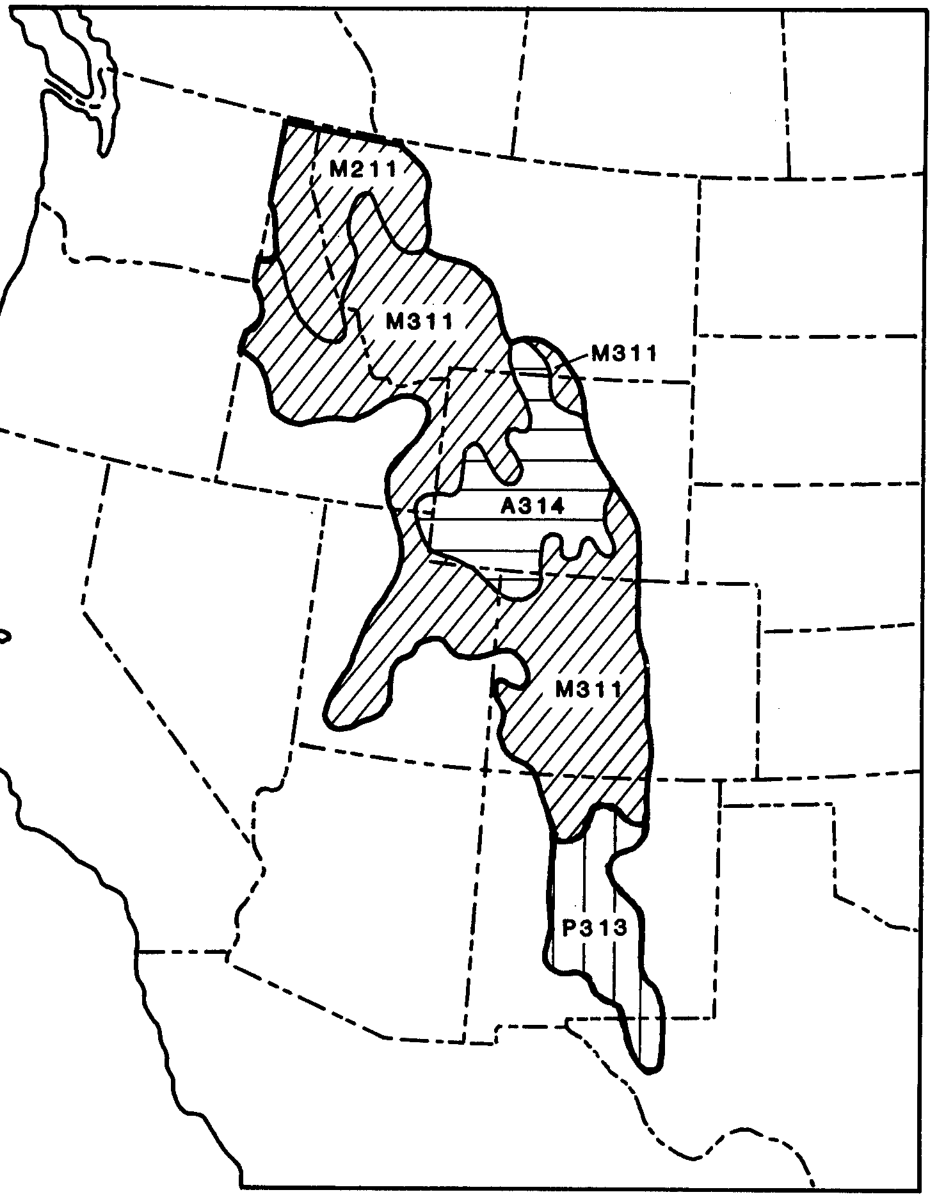


Figure 1. The geographic extent of this profile follows the ecoregion concept of Bailey and Cushwa (1981) and includes the Southern, Central, and Northern Rocky Mountain Provinces (see text). Part of Province M211 that lies south of the United States-Canada border is also included.

The principal areas covered by this report fall into the following categories, as defined by Bailey and Cushwa (1981):

Dry Domain

Semiarid Steppe Regime Highlands Division
Rocky Mountain Forest Province (M311)
Colorado Plateau Province (P313)
Wyoming Basin Province (A314)

Humid Temperate Domain

Humid Warm-summer Continental Regime Division
Columbia Forest Province (M211)

The areal extent of this ecological characterization encompasses a belt 2,000 km (1,240 mi) long and 200 km (124 mi) to 800 km (497 mi) wide (Wright 1983). The lowest place in the region is 970 m (3,200 ft) elevation in the Helena Basin in Montana. The highest point in the region is Mt. Elbert in the Sawatch Range west of the Arkansas Valley in Lake County, Colorado at 4,399 m (14,431 ft) elevation.

Composed for the most part of a complex series of separate mountain ranges, the Rocky Mountains are a major physiographic and climatic region separating the high plains grasslands of the Midwest from the high, cold deserts of the Colorado Plateau and Basin and Range Province ecotypes (Figure 1). Within this region, there are 108 mountain ranges (Table 1) and 33 intermountain basins (Table 2). Parts of the Rocky Mountains form the Continental Divide, which separates the principal drainage basins of the Atlantic and Pacific Oceans.

Within the conterminous United States, the Rocky Mountains can be conveniently divided into three major regions: the southern, central (middle), and northern (Figure 2). The southern Rocky Mountains are composed mostly of north-south trending ranges and extend from southeastern Wyoming into southern New Mexico and Arizona. The eastern ranges (Laramie, Snowy, Front, Wet, Culebra, Sangre de Cristo, and Sacramento) are separated from the western ranges (Park, Gore, Sawatch, Elk, San Juan, La Plata, and Jemez) by five major intermountain basins (North, Middle, and South Park; Arkansas River Valley; and San Luis Valley) as well as by several minor basins. For the purposes of this report, the mountains of the Pecos Highland also are included in the southern Rocky Mountains.

The central (middle) and southern Rockies are separated by the Wyoming Basin, often called the Red Desert, which is a large intermountain tectonic basin that contains only a few low ridges in a large expanse of otherwise gently rolling topography. The central Rockies occur mainly in Wyoming and include three main mountain groups. The eastern group includes the Bighorn and Beartooth Ranges (Figure 2). The western group is made up of Absaroka, Teton, Gros Ventre, Wyoming Ranges and the Yellowstone Plateau in Wyoming and the Wasatch and Uinta Mountains in Utah. A central group, composed of the Wind River and Owl Creek Ranges, cuts diagonally across central Wyoming and separates the Wyoming Basin on the south from the Bighorn Basin on the north.

Table 1. Mountain ranges of the Rocky Mountain region.

IDAHO	
Selkirk Range	In the northwest corner of the State.
Cabinet Mountains	Trend southeast from the Selkirk Range into Montana.
Clearwater Mountains	Between the Clark Fork of the Columbia River and the Clearwater River in northern Idaho.
Seven Devils Mountains	On the west-central boundary with Oregon south of the Salmon River.
Salmon River Mountains	South of the Salmon River and northwest of the Stanley Valley.
Sawtooth Mountains	Southwest of Stanley Valley.
Boulder Mountains	East of Stanley Valley.
Smokey Mountains	Southeast of the Sawtooth Range.
Soldier Mountains	South of the Sawtooth Range.
Hawley Range	East of the Boulder Mountains and the east fork of the Salmon River.
Lemhi Range	Parallels the Hawley Range on the east.
Bitterroot Mountains	Form eastern border with Montana north of the Beaverhead Range.
Beaverhead Range	Forms southeast part of border with Montana.
Centennial Range	Forms north border with Montana, just west of Wyoming.
Bannock Range	In southeastern corner of the State.
Port Neuf Range	Parallels the Bannock Range on the east.
Aspen Range	Parallels the Port Neuf Range on the east.
Caribou Range	Parallels the Aspen Range on the east.
Snake River Mountains	Parallels the Caribou Range on the northeast; extends into Wyoming.

Table 1. (Continued)

MONTANA	
McGillvray Mountains	North and east of the Cabinet Mountains; northern part extends into Idaho.
Flathead Mountains	Northwestern corner of the State.
Galton Range	Parallels the Flathead Mountains on their northeast.
Whitefish Range	Parallels the Galton Mountains on their east.
Lewis Range	Parallels the Whitefish Range on its east; contains Glacier National Park.
Swan Range	South of Whitefish Range and west of Lewis Range.
Mission Range	South of Flathead and Galton Ranges; parallels into Swan Range on its west.
Garnet Range	An east-west range between south end of Mission Range and southern part of Lewis Range.
Sapphire Mountains	Parallel the Bitterroot Mountains on their east.
Flint Creek Range	Trends SW-NE southeast of the Sapphire Mountains.
Pioneer Range	A N-S range just south of the Flint Creek Range.
Tendoy Mountains	A small range just north of the contact between the Beaverhead Range and the Centennial Range.
Ruby Range	A SW-NE trending range between the Tobaccoroot Range on the northeast and the Centennial Range on the south.
Tobaccoroot Range	Northwest of the Madison Range.
Madison Range	Extends north from the northwest corner of Wyoming.
Gallatin Range	Parallels the Madison Range on its east and extends south into northwest Wyoming.
Snowy Range	A massif east of the Gallatin Range that borders Wyoming.
Bridger Mountains	North of the Gallatin Range.

Table 1. (Continued)

MONTANA (con't.)	
Crazy Mountains	A massif east of the Bridger Mountains.
Castle Mountains	A small massif between the Bridger Range and the Little Belt Mountains.
Big Belt Mountains	Parallels the south end of the Lewis Range on its east.
Little Belt Mountains	A massif east of the Big Belt Mountains.
Big Snowy Mountains	A small range east of the Little Belt Mountains.
Judith Mountains	North-northeast of the Big Snowy Mountains.
Highwood Mountains	Northeast of the Little Belt Mountains.
Bearpaw Mountains	Northeast of the Highwood Mountains.
Little Rocky Mountains	East of the Bearpaw Mountains.
WYOMING	
Yellowstone Plateau	In the northwest corner of Wyoming, south of the Gallatin Mountains; contains Yellowstone National Park.
Absaroka Range	East of the Yellowstone Plateau and south of the Snowy Range.
Teton Range	Along the west boundary of Wyoming south of Yellowstone Plateau; includes Teton National Park.
Gros Ventre Mountains	A NW-SE trending range between the Tetons and the Wind River Range.
Wind River Range	South of the Absaroka Range, on the northeast edge of the Bridger Basin and northwest edge of the Red Desert.
Salt Range	Along the west boundary of Wyoming south of the Tetons.
Wyoming Range	Parallels the Salt Range on its east.
Hoback Range	Parallels the north end of the Wyoming Range on its east.

Table 1. (Continued)

<u>WYOMING</u> (con't.)	
Green Mountains	Trend NW-SE from the Wind River Range.
Ferris Mountains	Trend NW-SE from the Green Mountains.
Seminole Mountains	Trend NW-SE from the Ferris Mountains.
Freezout Mountains	Extend east form the Seminole Mountains into the Shirley Basin.
Granite Range	Parallels the Green Mountains on their northeast.
Rattlesnake Range	Parallels the Granite Range on their northeast.
Owl Creek Range	Parallels the Wind River Range on its northeast; encloses the southern end of the Big Horn Basin.
Big Horn Range	Trends NW-SE from southern Montana into central Wyoming; encloses the Big Horn Basin on the east.
Laramie Range	Trends north-south from the North Platte River in the southeastern part of Wyoming to the Colorado border.
Medicine Bow Mountains	Parallel the Laramie Range on its west; extend into northern Colorado; the Wyoming portion of these mountains is sometimes called the Snowy Range.
Sierra Madre	Trends west-northwest/south-southeast west of the Medicine Bow Mountains to the Colorado border.
Elk Mountains	North of the Medicine Bow Range.
<u>UTAH</u>	
Wasatch Mountains	Trend north-south through north-central Utah.
Wasatch Plateau	Parallels the southern Wasatch Mountains on their east.
Uinta Mountains	Trend east-west from northeast Utah to northwest Colorado.
La Sal Mountains	On the eastern border of Utah south of the Colorado River.

Table 1. (Continued)

<u>COLORADO</u>	
Park Range	Trends north-southwest of the center of the State; borders North Park on the west.
Flattop-White River Plateau	A massif southwest of the Park Range.
Battlement Mesa	South of the Flattops and of the Colorado River.
Grand Mesa	East of the confluence of the Colorado and Gunnison Rivers.
Uncompahgre Plateau	Trends NW-SE southward from the Colorado River at the State boundary.
San Juan Mountains	A large massif composed of several smaller ranges in the southwestern part of Colorado that extend south into north-central New Mexico.
La Plata Mountains	A small massif southwest of the San Juans.
San Miguel Mountains	North of the La Plata Mountains.
La Garita Mountains	A small range that trends northeast from the San Juans to the west edge of the San Luis Valley.
Sangre de Cristo Range	A north-south trending group of ranges that extends from the Arkansas River along the east side of the San Luis Valley into northern New Mexico.
Wet Mountains	Parallel to the northern part of the Sangre de Cristo on its east.
Spanish Peaks	Extend east from the center of the Sangre de Cristo.
Park Plateau	Extends east along the Colorado/New Mexico border from the Sangre de Cristo.
Sawatch Range	Trends north-south from the north end of the San Luis Valley; contains the highest peak in the Rocky Mountains - Mt. Elbert.
Gore Range	Between the Park and Sawatch Ranges; borders Middle Park on the west.
Elk Mountains	A massif north of the Gunnison River.

Table 1. (Continued)

COLORADO (con't.)	
West Elk Mountains	Extend northwest from the center of the Sawatch Range.
Mosquito Range	Parallels the north end of the Sawatch Range on its east.
Ten-Mile Range	Extends north from the Mosquito Range.
Front Range	A group of north-south trending ranges that face the Great Plains, extending from the Arkansas River on the south to the Wyoming border; includes part of Rocky Mountain National Park.
Never Summer Mountains	Parallel to the north end of the Front Range on its west; includes part of Rocky Mountain National Park.
Rabbit Ears Mountains	Trend east-west between the Park Range and the Never Summer Mountains; borders southern end of North Park.

NEW MEXICO

Some delineations of the Rocky Mountains stop with the Sangre de Cristo Mountains. There are several ranges through the center of the State in which the vegetation is clearly Rocky Mountain in character and where wetlands occur. These ranges are included here. They are more widely spaced than in the States to the north. Large plateaus extend from or separate several of these ranges. The vegetation of these plateaus is a mixture of mountain and desert plants, thus they are omitted from this listing.

Jemez Mountains	A massif south of the San Juan Mountains and the Chama River in the north central part of the State; includes the Sierra de los Valles.
Nacimiento Mountains	Border the Jemez Mountains on the west.
Mt. Taylor	Southwest of Jemez Mountains at southeast corner of the San Juan Basin.
Sandia Mountains	North-south trending southeast of Jemez Mountains on east side of Rio Grande.
Manzano Mountains	North-south trending south of the Sandia Mountains.

Table 1. (Concluded)

NEW MEXICO (con't.)	
Oscura Mountain	South of Manzano Mountains.
San Andres Mountains	South of Oscura Mountain and on west of Tularosa Basin.
Organ Mountains	South of San Andres Mountains.
Sierra Blanca	Trends north-south along the northeast part of Tularosa Basin.
Sacramento Mountains	South of Sierra Blanca along the east side of Tularosa Basin.
Datil Mountains	A massif south of Mt. Taylor.
Magdalena Mountains	Extend south from the east end of the Datil Mountains.
San Mateo Mountains	Parallel the Magdalena Mountains on the west.
Sierra Mimbres	South of the Datil Mountains.
Fra Cristo Mountains	Parallel the northern Sierra Mimbres on the east.
Caballos Mountains	Parallel the southern Sierra Mimbres on the east.

Table 2. Intermountain basins of the Rocky Mountain region. (After Atwood 1945.)

IDAHO	
Stanley Valley	In Northern Idaho, bounded by Sawtooth Range on west, Boulder and Whitecloud Mountains on east and south, and by Salmon Mountains on north and east.
Bitterroot Basin*	Between Bitterroot Mountains on west and Sapphire Mountains on the east.
Salmon River Basin	Between Beaverhead and Lemhi Ranges.
Teton Valley	Tetons on the east and Big Hole Mountains on west.
MONTANA	
Kalispell Basin*	Flathead Lake area, bounded on east by Lewis Range and on west by Bitterroot Mountains and Flathead Range.
Helena Basin*	Bounded by Big Belt Mountains on east and a nameless range on west.
Crazy Mountains Basin	Bounded by Madison Range on south, Bridger Range on the east and nameless mountains on the west.
WYOMING	
Wyoming Basin	Between the Laramie Range on the south and the Big Horn Mountains on the north and west.
Red Desert Basin	Between the Salt Range and Gros Ventre Mountains on west, the Wind River Range on the northeast and the Park Range on the southeast.
Wind River Basin	Between the Wind River Range on the southwest and the Casper Arch on the northeast.
Washakie Basin	South of the Red Desert on the Wyoming/Colorado border.
Bridger Basin (Green River Basin)	In the southwest corner of Wyoming.

Table 2. (Continued)

Great Divide Basin	Between the Laramie Range on the east and northern Snowy Range on west.
Shirley and Laramie Basins	South-central, bounded by Laramie Range on east and Snowy Range on west, and separated by a low pass.
Big Horn Basin	Between the Big Horn Mountains on the east and the Wind River Range on the west.
Powder River Basin	Bounded on the east by the Black Hills and on the west by the Big Horn Mountains.
Jackson Hole	Between the Gros Ventre Mountains on the east and the Tetons on the west.
<u>COLORADO</u>	
Gunnison Basin	Bounded on east by the Sawatch Range, on the south by the La Garitas, on the north by the West Elk Mountains, and on the west by the Elk Mountains.
Las Animas Basin*	From Coal Bank Pass in the San Juan Mountains south to Farmington, New Mexico, between the San Juans on the east and the La Plata Mountains on the west.
Middle Park	Bounded on southwest by the Gore Range, on east by the Front Range, and on the north by the Park Range and Never Summer Mountains.
Montrose Basin*	From the Grand Mesa south to the San Juan Mountains, with the Uncompahgre Plateau on the southwest and the Elk Mountains on the east.
North Park	From the Never Summer Mountains and the Medicine Bow Range on the east to the Park Range on the west, with the Rabbit Ears Range on the south.
San Luis Valley	Bounded by the Sangre de Cristo Range on the north and east, the La Garita Range and South San Juan Mountains on the west. Extends into northern New Mexico.
South Park	Bounded by the Tarryall Mountains on the east, Buffalo Peaks and Mosquito Range on the west, Kaufman Ridge on the south and an extension of the Front Range on the north.

Table 2. (Concluded)

Eagle/Walcott Basin*	South of the White River Plateau, west of the north end of the Sawatch Range, and contains the Eagle and Colorado Rivers.
Wet Mountain Valley	Between the Wet Mountains on the east and the Sangre de Cristo Range on the west.
Yampa Basin	Bounded on the south and west by the Flattop Mountains and on the north and west by the Park Range.
NEW MEXICO	
San Juan Basin	Northwest corner, bounded on north by La Plata Mountains and Mesa Verde, on the south by the Zuni Mountains, on the southeast by Mt. Taylor, and on the west by Defiance Plateau and Chuska Mountains.
Sandia Basin*	Bounded on east by Sandia and Manzano Mountains, on west by Mt. Taylor and Mesa Lucera, and Ladrone Peak on south.
Elephant Butte Basin*	Bounded on east by Caballos and Fra Cristo Mountains and on west by Sierra Mimbres.
Tularosa Basin	Between the San Andres and Sacramento Mountains in southern region.
Jornada del Muerto	Between the San Andres and Caballos Mountains.
Estancia Valley	Between the Manzano Mountains and the Pedernal Hills.

*Denotes names given by this publication to areas that do not now have an official geographic name.

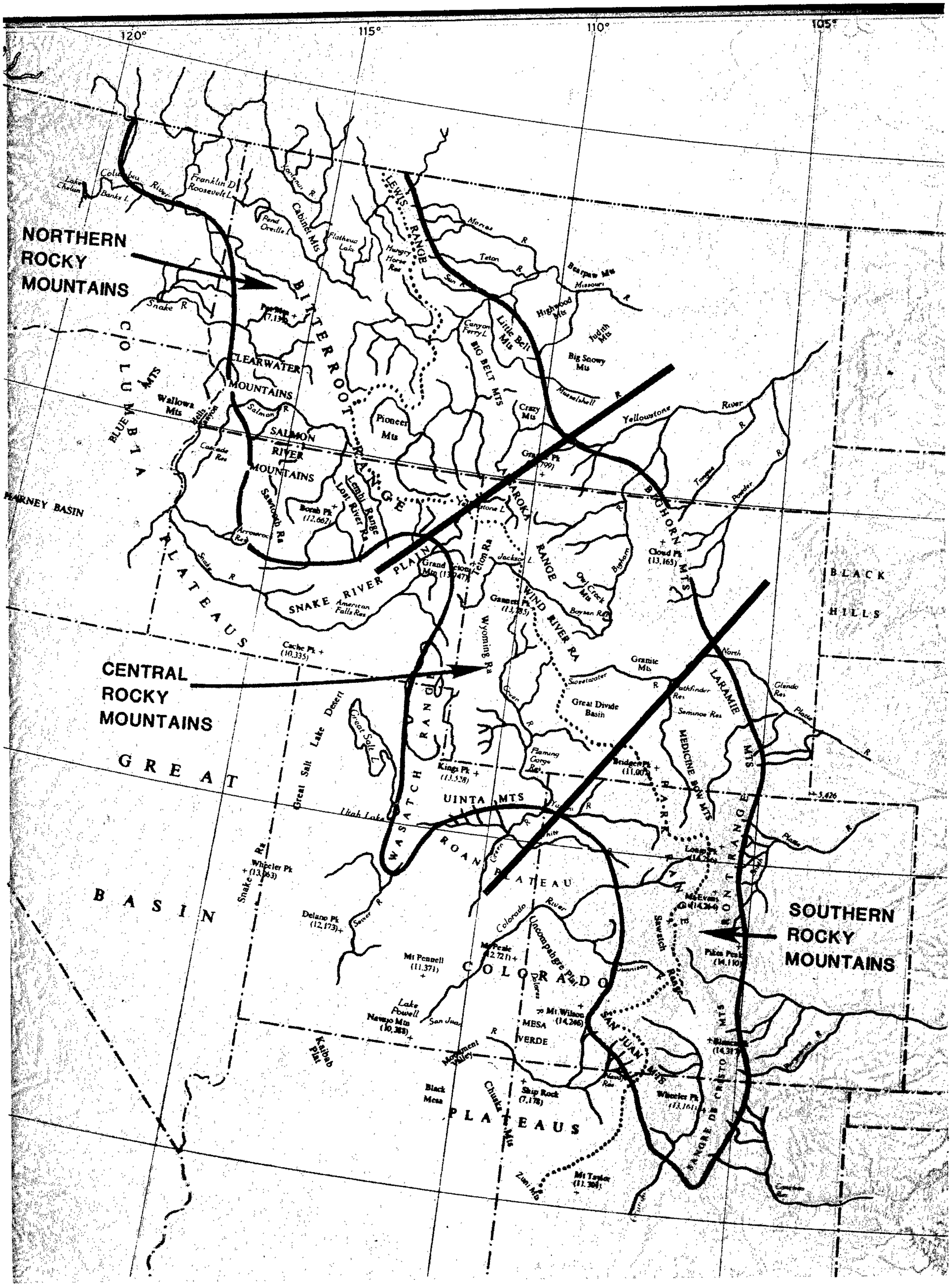


Figure 2. Physiographic map of Rocky Mountains. (Adapted from Hunt 1967 and U.S.D.I., Geological Survey 1970.) This report also includes ranges in New Mexico that have Rocky Mountain vegetation characteristics.

The northern Rockies are more compact geographically, but include several mountain ranges of diverse origins. The ranges in western and central Idaho are formed of the granite of the Idaho Bitterroots batholith. Nearby, mountains in southwestern Montana are fault-block types and not granitic. Bordering the Great Plains are the primarily sedimentary and volcanic ranges of Montana, the northern portions of which are similar to the Canadian Rockies, and the southern portion more like the ranges of northwestern Wyoming. The Montana ranges are separated by intermountain basins that are much narrower and more valley-like than the basins in the central and southern Rocky Mountains.

Five major river systems rise in the Rocky Mountains: the Columbia and the Colorado on the Pacific Slope; the Missouri, Red, and Rio Grande on the Atlantic Slope (Table 3a).

Several large natural lakes are encompassed in the region (Table 3b). Most are freshwater, moraine-dammed lakes, including Grand Lake, Colorado; Jackson Lake, Yellowstone Lake, and Three Rivers Lake, Wyoming; Bear Lake, Utah; Couer d'Alene Lake, Idaho; Upper and Lower St. Mary's Lakes and Flathead Lake, Montana. One lake, Great Salt Lake, Utah, is a large saltwater body landlocked at the western base of the central Rocky Mountains, which is primarily dependent on rivers from the Rocky Mountains for its major water input. This lake is a remnant of Lake Bonneville, one of several landlocked Pleistocene pluvial lakes in the Great Basin.

Several large mountain valleys held moraine-dammed lakes at various times during the postglacial periods of the Pleistocene and now are wetlands in various stages of succession (Table 3c).

1.4 ROCKY MOUNTAIN ECOSYSTEMS

The abrupt elevational rise of the Rocky Mountains results in clearly visible ecosystem changes with increasing elevation. These changes are more sharply defined than changes in most sections of the United States (Merriam 1890, 1894, 1898; Marr 1967). Mountain ecosystems tend to be ordered in predictable patterns on the landscape. The flora and fauna of mountain ecosystems tend to be limited to sites where they can best utilize local resources. These ecosystem regions (Marr 1967) or life zones (Merriam 1890, 1894, 1898) are characterized according to a given range of temperature, humidity, type and amount of precipitation, growing season length, amount and distribution of wind, and soil conditions. Life zones are higher in elevations on south-facing slopes than they are on north-facing slopes, due to increased solar flux received on south-facing slopes, which alters the interactions with other site factors.

Four life zones are recognized in the Colorado Rockies (Marr 1967): Alpine (above treelimit), Subalpine, Upper Montane, and Lower Montane (or Foothills adjacent to the Great Plains or the high cold desert). Only wetlands in the Subalpine, Upper, and Lower Montane zones are addressed in this report. Alpine wetlands have a different character because they are generally underlain by permafrost and grow in an Arctic, rather than temperate climate region.

Table 3. Rivers, natural lakes, and glacial lake basins of the Rocky Mountain region.

3a. Major rivers that rise in the Rocky Mountains, with their major tributaries.

Missouri River

- Yellowstone
- Platte
- Mussellshell
- Big Horn

Colorado River

- Green
- Dolores
- Eagle
- Gunnison
- San Juan

Columbia River

- Snake
- Clearwater
- Salmon

Red River

- Arkansas

Rio Grande

- Pecos

3b. Major glacial and pluvial lakes of the Rocky Mountain region.

Large Natural Lakes

- Coeur d'Alene Lake, ID
- Grays Lake, ID
- Priest Lake, ID
- Lake Pend Oreille, ID
- Flathead Lake, MT
- Upper and Lower St. Marys Lakes, MT
- Lake Sherburne, MT
- Lake McDonald, MT
- Waterton Lake, MT/Canada
- Bowman Lake, MT
- Kintla Lake, MT
- Jackson Lake, WY
- Yellowstone Lake, WY
- Shoshone Lake, WY
- Jenny Lake, WY
- Heart Lake, WY
- Lewis Lake, WY
- New Forks Lake, WY
- Willow Lake, WY
- Boulder Lake, WY
- Fremont Lake, WY
- Grand Lake, CO
- Twin Lakes, CO
- Bear Lake, UT
- Great Salt Lake, UT*
- Laguna del Perro, NM

3c. Examples of Colorado valleys that once held large moraine-dammed lakes.

- Kawuneeche Valley, CO
- Moraine Park, CO
- Horseshoe Park, CO
- Upper Roaring Fork Valley, CO
- Crystal River Valley, CO
- Upper San Juan, west of Wolf Creek Pass, CO
- Upper Las Animas River Valley, CO
- Upper Slate Creek Valley, CO
- Upper Arkansas Valley, CO

*Included because of its origins from Rocky Mountain runoff and its wetlands that resemble some in Rocky Mountain intermountain basins.

In general, life zones form altitudinal belts around the Rocky Mountains and, regardless of whether the mountains are approached from the east, west, north, or south, one will pass through each belt. The elevational range and width of each life zone decreases with increasing latitude. Most mountain wetland ecosystems change in consistent ways from the lowlands to the mountain tops. For example, wetland-adapted species in the highest life zones are adapted to survive a very short growing season and long periods of snow cover. Species in the lower life zones have a growing season up to twice as long, and are adapted to survive in areas of lesser precipitation, and some are adapted to frequent drought.

Each of the life zones is characterized by a specific set of dominant plants that distinguishes it from other life zones (Table 4). For example, in the Colorado Front Range, the Lower Montane Life Zone is dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) with scattered Rocky Mountain juniper (*Juniperus scopulorum*). Mountain mahogany (*Cercocarpus montana*), blue grama grass (*Bouteloua gracilis*), and other grasses, shrubs, and herbs form an understory (Marr 1967). The Upper Montane Life Zone also is dominated by ponderosa pine and Douglas-fir, but lodgepole pine (*Pinus contorta*) and quaking aspen (*Populus tremuloides*) form dense secondary successional forests in response to disturbances, e.g., fire and clearing. Neither of these species grows in the lower elevations. In the Subalpine Life Zone, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) form the ecosystem climax dominants, and lodgepole pine and aspen again are successional trees (Marr 1967). Limber pine (*Pinus flexilis*) forms forests on exposed ridge tops; Marr (1967) considers these stands topoedaphic climax. Table 5 summarizes climatic factors, elevations, and dominants of each life zone, as reported by Marr (1967) for the Colorado Front Range.

Boundaries between adjacent life zones are rarely sharp and distinct. Interdigitation of life zones and mixing of adjacent ecosystems is common where life zones meet. The transitional areas between life zones, called ecotones, are characterized by a gradation of physical factors, which results in a mixture of flora and fauna from the two adjacent ecosystems. The most striking ecotone is that between the Subalpine and the Alpine, where the tall, erect forest trees become dwarfed, contorted and grow further apart.

Elevation limits of the different life zones vary considerably from south to north, and according to slope exposure (Tables 4 and 6). For example, going northward from the southern Rocky Mountains to the northern Rocky Mountains, lower limits of each life zone shift progressively downward in elevation. Treelimit elevation decreases approximately 110 m (360 ft) for every degree of latitude northward. Roughly, a climb of 305 m (1,000 ft) is equivalent to a distance of 965 km (600 mi) to the north. Treelimit averages around 3,721 m (12,200 ft) elevation in northern New Mexico and southern Colorado; in northern Colorado, it is around 3,477 m (11,400 ft); in Wyoming, it is around 2,898 m (9,500 ft); and in northern Montana, it is around 2,288 m (7,500 ft). In Colorado, the subalpine forest containing wetlands extends up to 3,477 m (11,400 ft) in the northwest Rocky Mountains, whereas in the southeast, it extends up to 3,721 m (12,200 ft).

Table 4. Major changes in dominant vegetation with increasing latitude.[a]

Meters (ft)	Southern New Mexico	Northern New Mexico and Southern Colorado	Northern Colorado and Utah	Central Wyoming	Northern Idaho and Montana
3,660 (12,000)	(12,100) S: Corkbark fir Engelmann spruce Aspen	(12,000)			
3,355 (11,000)		S: Engelmann spruce Subalpine fir Bristlecone pine Aspen Corkbark fir	(11,400)		
3,050 (10,000)	UM: Southwestern white pine White fir Douglas-fir Aspen Blue spruce		S: Engelmann spruce Subalpine fir Limber pine		
2,745 (9,000)		UM: Ponderosa pine Douglas-fir Lodgepole pine Aspen Blue spruce		(9,500) S: Subalpine fir White-barked pine Engelmann spruce	
2,440 (8,000)			UM: Ponderosa pine Douglas-fir Lodgepole pine Aspen Limber pine	UM: Lodgepole pine Douglas fir Aspen	(7,500)
2,135 (7,000)	LM: Ponderosa pine Pinyon pine Junipers	LM: Ponderosa pine Douglas-fir Pinyon pine Junipers Gambel's oak	LM: Douglas-fir Ponderosa pine Rocky Mountain juniper Mountain mahogany Gambel's oak (in south)	LM: Grass Douglas-fir Limber pine Sage and other shrubs	S: Engelmann spruce Mountain hemlock Western larch White-barked pine
1,830 (6,000)	P: East: shortgrass plains West: high desert	P: East: shortgrass plains West: high desert			UM: Western hemlock Noble fir Grand fir Western red cedar Ponderosa pine Aspen
1,525 (5,000)			P: East: shortgrass plains West: high desert	P: East: shortgrass plains West: high desert	LM: Ponderosa pine Limber pine Douglas-fir Juniper
1,220 (4,000)					
915 (3,000)					P: East and West grasslands

[a] S = Subalpine
UM = Upper Montane
LM = Lower Montane (Foothills)
P = Plains/High Desert

Table 5. Climatic factors of ecosystems of the Front Range. (After Marr 1967.)

Regional ecosystems	Elevation range m (ft)	Air temperature (°C) (°F) max	X̄	min	Wind	Precipitation	Frost-free days
Lower Montane	1,829 to 2,347 (6,000 to 7,700)	36 (96)	8 (47)	-18 (-3)	11 (7)	51 (20)	137
Upper Montane	2,347 to 2,835 (7,700 to 9,300)	32 (89)	6 (42)	-22 (-7)	12 (7.5)	53 (21)	100
Subalpine	2,835 to 3,475 (9,300 to 11,400)	24 (75)	-26 (34)	16 (-14)	66 (10)	66 (26)	87

Table 6. Relationship of elevation of Rocky Mountain regional ecosystems (life zones) to latitude.

Latitudinal transect	Elevations in meters (ft) of: Lower Montane	Upper Montane	Subalpine	Treelimit
New Mexico/ Colorado border (37 degrees)	1,951-2,560 (6,400-8,400)	2,560-3,048 (8,400-10,000)	3,048-3,658 (10,000-12,000)	3,658 (12,000)
Northern Colorado (40 degrees) (Marr 1967)	1,829-2,347 (6,000-7,700)	2,347-2,835 (7,700-9,300)	2,835-3,475 (9,300-11,400)	3,475 (11,400)
Central Wyoming (43 degrees)	1,585-2,225 (5,200-7,300)	2,225-2,560 (7,300-8,400)	2,560-2,896 (8,400-9,500)	2,896 (9,500)
Southern Montana (46 degrees)	1,372-1,981 (4,500-6,500)	1,981-2,377 (6,500-7,800)	2,377-2,743 (7,800-9,000)	2,743 (9,000)
Northern Montana and Idaho (48 degrees)	1,067-1,615 (3,500-5,300)	1,615-2,073 (5,300-6,800)	2,073-2,286 (6,800-7,500)	2,286 (7,500)

Although few published data are available relating the north-to-south topographic exposure of wetlands, terrestrial ecosystems show considerable variation of distribution with exposure to sunlight. Slopes facing north receive considerably less direct sunlight than those facing south; consequently, they experience lower mean annual temperatures and are more wet and snowy. North-exposed wetland and terrestrial ecosystems also have much less direct sunlight, lose less water from evaporation, have longer periods of snow cover, and have a much shorter frost-free season. South-facing ecosystems receive the maximum solar flux in December and January when the sun is lowest on the horizon. This places high water stress on plants on these slopes. Evaporation rates are higher, snow melts much more rapidly, and there are more freeze-thaw cycles on south-facing slopes. These physical differences are great enough to cause major differences in the types of plants and ecosystems found on adjacent slopes with different exposures. For example, moss and lichen floras found on northern exposures are similar to those of northern coastal regions of southeastern Alaska and Norway. South-facing slopes have specific climates more like desert mountains and high cold deserts, with moss and lichen floras like those found in the Gobi Desert and the American southwest.

Furthermore, because of the moist Pacific fronts that travel west to east, western slopes of Rocky Mountain ranges receive more moisture and less wind than eastern slopes. This results in a more continuous snow cover on western slopes, which reduces the exposure of vegetation to cold temperatures and winds. By contrast, along the east slope of the mountains facing the Great Plains, temperatures can fluctuate as much as 22 °C (40 °F) in 2 hours. These fluctuations are brought about by warm, high westerly (Chinook) winds, often in excess of 193 kph (120 mph), that flow down the eastern slopes of mountains. These winds melt snow and increase transpiration from trees at periods when available water may be either absent or frozen (Marr 1967).

1.5 LOCATION OF ROCKY MOUNTAIN WETLANDS

The Rocky Mountain region is characterized by topographic, geological, climatological, and ecological heterogeneity creating a wide range of conditions in which wetlands have formed. Wetlands are found at all elevations throughout the Rocky Mountain region. However, wetlands of mountain valleys are distinguished from those of intermountain basins on the basis of distinctly different geological origins, weather, and resulting soil types of these two major topographical features.

Mountain valleys are relatively young topographical forms shaped by the erosional forces of running water and, at higher elevations, by glacial movements. Wetlands are located in a wide range of sites from cliff faces to gentle slopes to flat valley floors. A high water table is maintained by accumulation from melting snow and frequent summer storms, which interacts with variable depth of bedrock and permeable materials, such as moraines and other glacial till, that contain either surface or subsurface water.

Intermountain basins were formed by ancient tectonic and volcanic events contemporary with the mountain-building processes. Erosion of neighboring mountain ranges has contributed deep strata of alluvial material that are gradually filling large topographical depressions. Rivers have inscribed channels across the flat "parks" and have changed course or been impounded by

tectonic and volcanic alterations in basin geomorphology. Wetlands also are associated with river meander patterns, impounded waters, and high water table maintained by underlying aquifers, annual flooding, or impermeable substrates.

Mountain Valleys

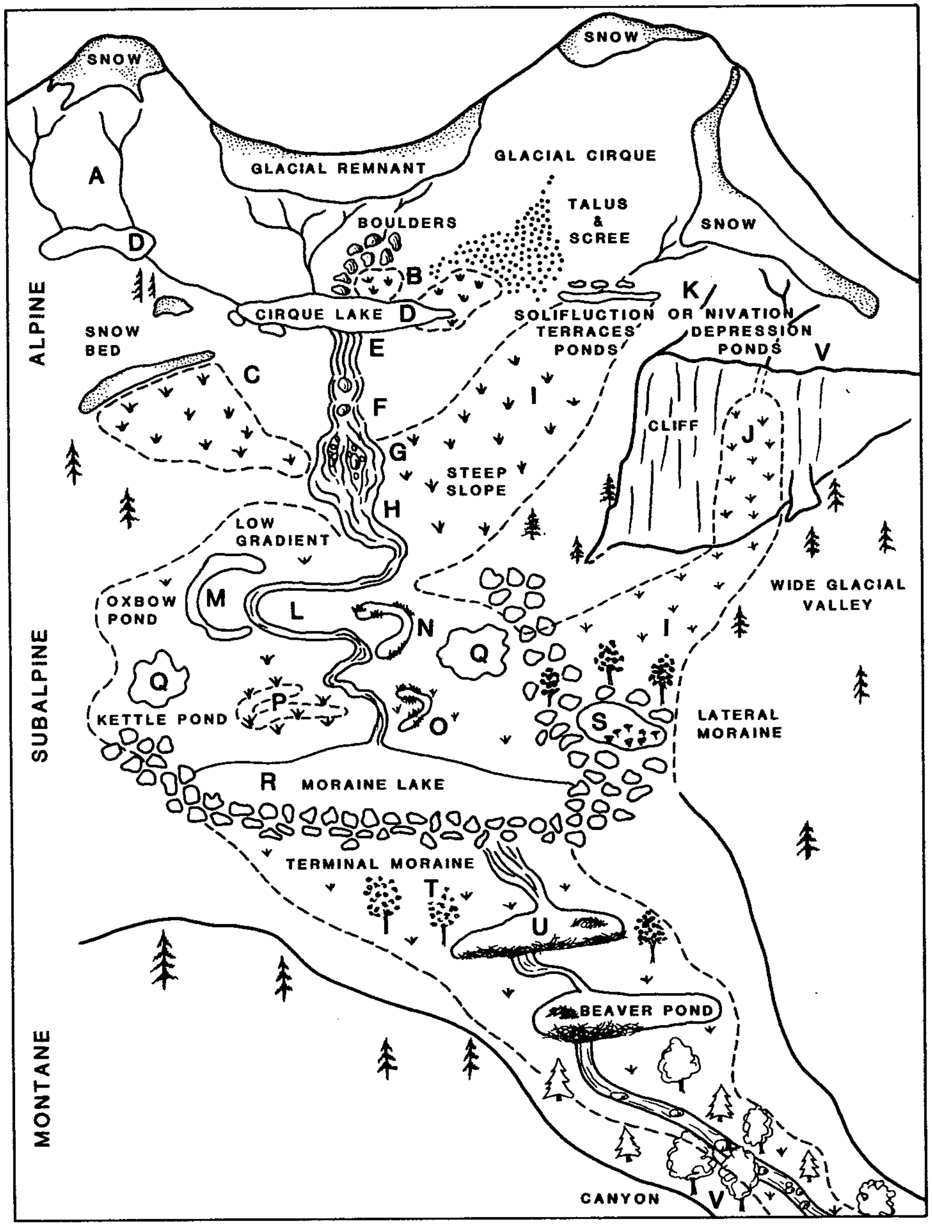
If one had a bird's eye view of a river drainage from the mountain peaks at its head, down-valley to the plains, or the intermountain basins, one could see common wetland types in relation to their physical surroundings. Such a view (Figure 3) is the focus of the following discussion of mountain valley wetland types and their locations.

Glacial action in high mountains has formed large cirque basins resembling amphitheaters in which snow collects and remains, sometimes into late summer. A few small remnant glaciers occur above some cirque basins. As water flows from melting snow and ice, it forms a multitude of small rivulets that coalesce into tributary streams (Figure 3A). They may disappear under porous boulder and talus fields, reemerging at the toe of slopes as trickling seeps or gushing springs (Figure 3B). Wetlands also form under and downslope of late-lying snowbeds (Figure 3C). Spring, seep, and snowbed wetlands are found at any elevation that has similar geomorphic conditions.

In many cirque basins, glaciers scoured away loosened rock at heads of valleys leaving depressions now filled by cirque lakes or "tarns" (Figure 3D) that are generally small and shallow (less than 50 m deep). Glacial lakes may be in step-like series, one on a shelf interconnected to the next lower one by waterfalls, cascades, riffles, and pools (Figure 3E-H). These lake chains (Figure 4) are called "string of beads" or "paternoster" lakes (Wetzel 1983).

Gently sloping willow- or sedge-dominated wetlands may occur at the sides of the valley (Figure 3I). Dripping cliff faces occasionally support patches of "hanging garden" wetlands (Figure 3J). At treelimit, nivation depressions and solifluction terraces create small ponded areas (Figure 3K). Nivation depressions (Figure 5B) form from a complex process involving the accumulated weight of deep snows interacting with saturated soils (Matthes 1900). Solifluction terraces and ponds (Figure 5A) form when saturated soils located over either permafrost or bedrock slump downhill creating shallow depressions (Zwinger and Willard 1972; Komarkova 1979; Willard 1979).

Below a hanging U-shaped valley, glaciers carve larger U-shaped valleys with flat gently sloping floors and nearly vertical walls (Figure 3V). Glacial deposits are bisected by a meandering stream (Figure 3L) and support a variety of wetland types. The history of the stream's meander migrations on the floodplain is seen from aerial view in the form of oxbow lakes with different wetland seral stages (i.e., of different ages). A new oxbow lake is mainly open water; slightly older oxbows fill with sedges (<u>Carex</u> spp., <u>Eleocharis</u> spp.), rushes (<u>Juncus</u> spp.), willows (<u>Salix</u> spp.) and other hydrophytes. The oldest oxbows support more mesic terrestrial vegetation (Figure 3M-P). Willows may form a climax ecosystem, which remains unchanged over time, in locations with a consistently high water table.



A. Tributary streams.
B. Seep and spring wetlands at the base of boulder, talus, and scree fields.
C. Snowbed wetlands.
D. Cirque or tarn lakes.
E. Waterfall.
F. Cascade.
G. Riffles in braided stream.
H. Pool.
I. Sloping willow-shrub wetland.
J. "Hanging garden" or cliff wetland.
K. Nivation depression or solifluction terrace pools.
L. Meandering stream in wide glacial valley.
M. Newly formed oxbow lake.
N. Early seral stage (emergent sedge/rush) in oxbow lake.
O. Later seral stage (sedge/willow) in oxbow lake.
P. Climax seral stage (willow/carr) in oxbow lake.
Q. Kettle lakes.
R. Moraine lake (pond) created by terminal moraine.
S. Moraine lake (pond) (semidrainage lake) in lateral moraine.
T. Seeps and spring wetlands at foot of moraine.
U. Beaver pond wetlands.
V. Narrow canyon riparian wetland.

Figure 3. Wetland types and their location within the upper end of a mountain valley. (By S. Q. Foster.)

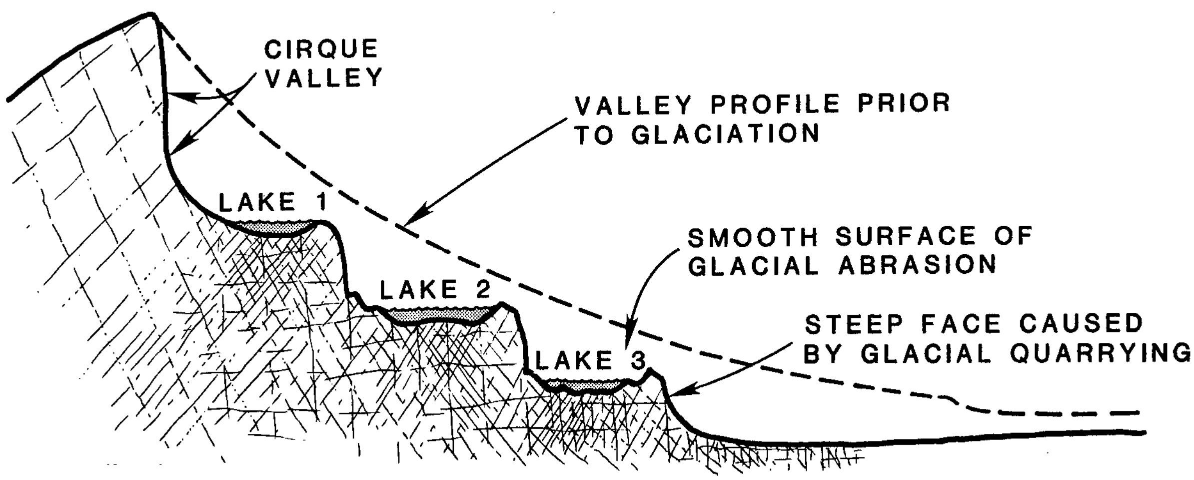


Figure 4. Longitudinal profile and section of a glacially carved valley holding paternoster lakes in glacially abraded steps separated by glacially quarryed cliffs. Steps are produced by unequal distribution of joints and other planes of weakness in bedrock alternating with massive bedrock under the lakes. Valley profile prior to glaciation is indicated by a dashed line. (Adapted from Longwell, Knopf, and Flint 1939.)

As glaciers retreat, large ice chunks break off at the toe and are buried in glacial outwash deposits on the valley floor (Figure 6). When the ice chunks melt, a depression forms that fills with water and becomes a glacial kettle. These kettle lakes are usually less than 50 m deep, and often correspond in shape to the original ice block (Wetzel 1983). Kettle lakes, like other lakes, pass through wetland seral stages (Figure 3Q).

Moraine lakes are common in the Rocky Mountains wherever retreating glaciers left mounds of rock debris (terminal and lateral moraines) (Figure 3R). Terminal moraines usually blocked stream channels; resulting impoundments are evident today as either a moraine lake, a high mountain meadow or "park," or some seral stage between the two. Twin Lakes and Grand Lake in Colorado both occupy basins formed by a combination of bedrock features and a lateral/terminal moraine complex (Figure 7). Small moraine and semidrainage lakes may be found in irregular depressions among lateral and terminal moraines (Figure 3S). Wetlands also may occur in seeps and springs at the base of moraines (Figure 3T).

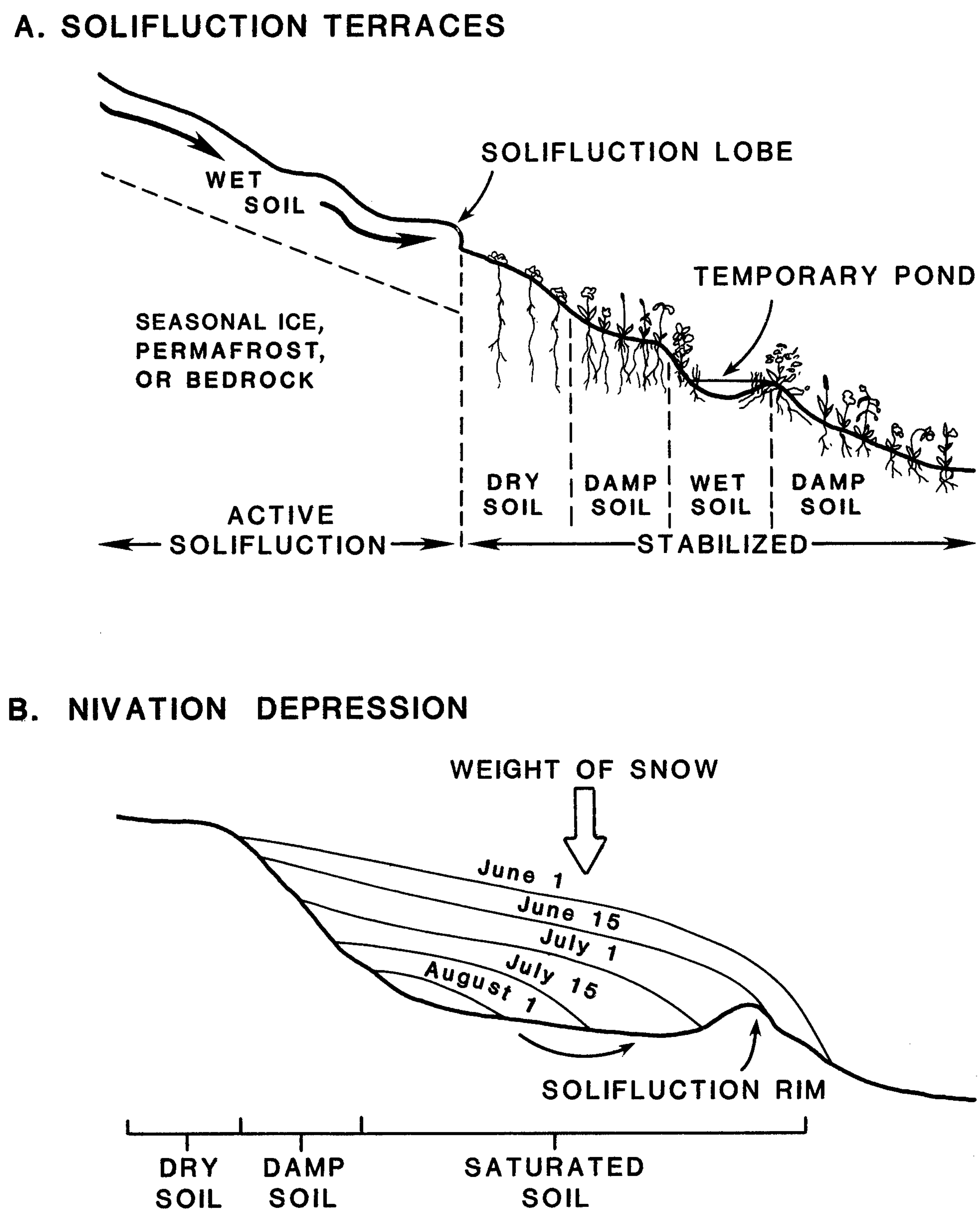


Figure 5. Small pools may form near treelimit: (A) behind solifluction terraces formed by downhill movement of wet soil overlaying permafrost or bedrock; and (B) in shallow pockets (nivation depressions) as a heavy snowbed presses down on saturated soils and permafrost maintains a high water table. (Adapted from Zwinger and Willard 1972.)

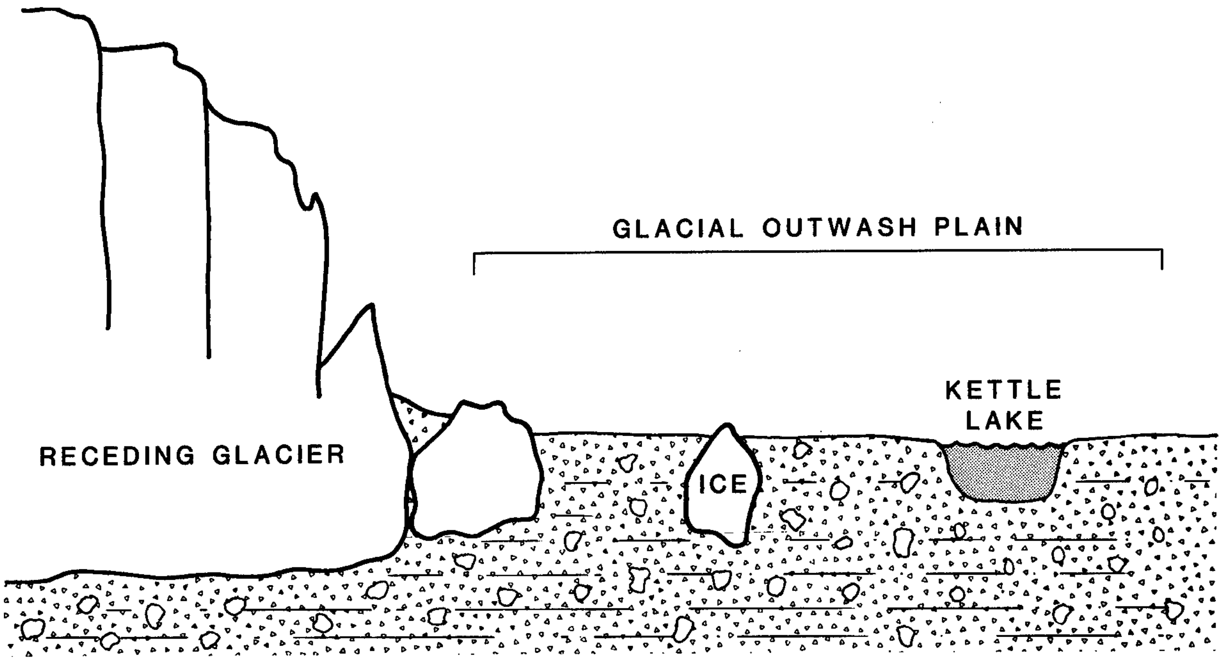


Figure 6. Kettle lakes form on glacial outwash plain as buried chunks of glacial ice melt and form ponds in the glacial till. (From Wetzel 1983.)

Large flat wet areas, such as Moraine and Horseshoe Parks in Rocky Mountain National Park, are the result of large moraine lakes that have gradually been filled by glacial outwash and alluvium (Figure 7), which eventually displaced the water (Wetzel 1983). Mountain parks and meadows formed in this way tend to be wide, flat valleys characterized by a meandering stream and lush vegetated wetlands.

Series of shallow beaver ponds are commonly found in montane and subalpine valleys (Figure 3U). The collective activities of beaver have transformed large regions of the Rocky Mountains into wetlands that support wildlife, fish, and many plants (Ives 1942b; Grasse 1951; Arner 1963; Brayton 1983).

In unglaciated valleys at lower elevations, rivers have incised V-shaped canyons in which floodplain development is limited (Figure 3V). Riparian wetlands in these valleys form narrow ribbons of vegetation that change species composition with elevation (Figure 8). For example, in Colorado, between 2,898 m (9,500 ft) and treelimit, 3,508 m (11,500+ ft), willows persist. In middle elevations, from 2,288 m to 2,806 m (7,500 to 9,200 ft), riparian wetlands may be dominated by narrow-leaf cottonwood (_Populus angustifolia_), Colorado blue spruce (_Picea pungens_), alder (_Alnus tenuifolia_), river birch (_Betula fontinalis_), willows (_Salix_ spp.), and red-osier dogwood (_Swida sericea_). At lower elevations, from 1,678 m to 2,135 m (5,500 to 7,000 ft), narrow-leaf cottonwood and Colorado blue spruce are replaced by plains cottonwood (_Populus sargentii_), box-elder (_Acer negundo_), and different willows.

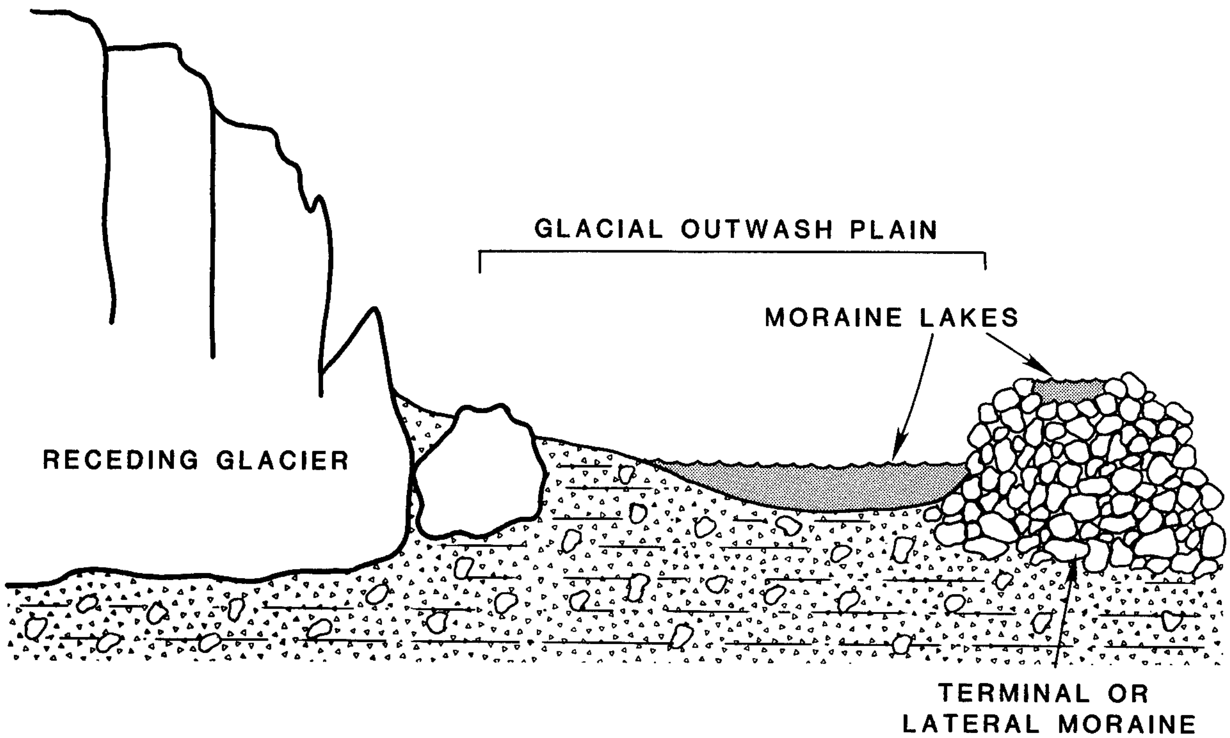


Figure 7. Moraine lakes form in depressions up-valley of terminal and lateral moraines left behind by receding glaciers. (From Wetzel 1983.)

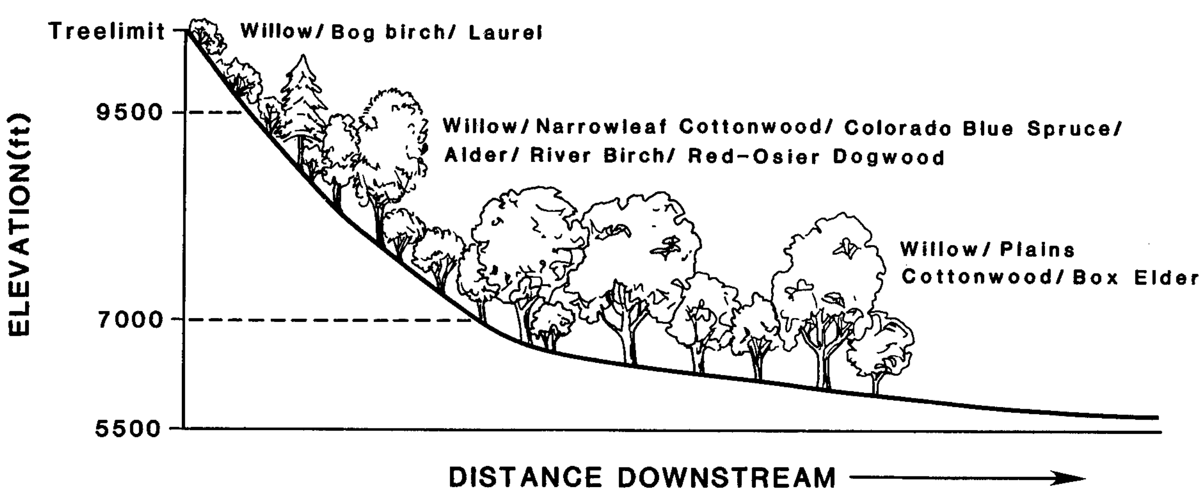


Figure 8. Streamside (riparian) plant community composition changes with elevation (as found in Colorado). (By S. Q. Foster.)

Intermountain Basins

Intermountain basins occur between and among major mountain ranges throughout the Rocky Mountains (Atwood 1945) (Table 2). Intermountain basins are large topographic depressions of tectonic origin with level to gently rolling topography; they are many miles in length and width. These basins are underlain by thick alluvial deposits lying on bedrock. Anticlines, synclines, hogbacks, faulting, and volcanic intrusions are evidence of their individual and complex tectonic histories. Soils in these intermountain basins are very different physically and chemically from soils on surrounding mountains.

Dominant vegetation types are either shrubs or graminoids with some forbs. Wetland-adapted plants, such as sedges, rushes, and willows, may predominate for hundreds of hectares. Many wetlands in these basins are alkali flats, marshes, and lakes associated with tectonic disruption of drainage. Table 7 gives the latitude and general elevation of each basin, together with major dominant plants.

Local weather in these basins differs from that in the surrounding mountains, especially in range of temperature, amount of precipitation, and fetch and velocity of winds that desiccate the areas and blow snow from surfaces of basins into drifts. Weather patterns are affected by the large, nearly level basin surfaces that heat up and cause updrafts that dissipate clouds and also create convectional storms. Solar insulation is more constant and less affected by topography, therefore, there are fewer effects of exposure.

The San Luis Valley of southern Colorado is an example of an intermountain basin. Its geological structure is illustrated in cross-section in Figure 9. Note that originally flat-lying Paleozoic sedimentary rocks were warped and broken during the tectonic processes of mountain building, and volcanic activity has further transformed the landscape. The valley has accumulated additional sedimentary material in recent times (Oetking et al. 1967).

In plan view (Figure 10), the valley is bounded on all sides by mountain ranges from which streams transport water and alluvium to the basin floor, either into lakes lacking outlets or to the Rio Grande River. It has been estimated that there are 3,600 wetlands occupying 220.8 square miles (5.5%) of the 4,000 square mile basin (U.S.D.I. Fish and Wildlife Service 1955).

Historically, many wetlands in the San Luis Basin were wet only during short periods of natural spring runoff. Today, canals, irrigation seeps, return flows, and artesian wells contribute to the formation and maintenance of wetlands. An active, internally drained sump region located along a major fault zone in the northeastern part of the valley supports a large wetland acreage (McCalpin 1981).

Intermountain basins are intensely used for agriculture, grazing, and human settlement, as well as wildlife refuges. In many of them, the original types and extent of wetlands are not known. Over-irrigation has been beneficial in some areas by creating wetlands of value to migrating, nesting, and wintering birds and other wildlife. Irrigation storage in reservoirs and wetland drainage has reduced wetland habitat in other areas.

Table 7. Latitude, elevation, and dominant plants in intermountain basins of the Rocky Mountains.

Intermountain basins	Latitude (degrees N)	General elevation m (ft)	Dominant species
IDAHO			
Stanley Valley	44 - 44.2	1,830 (6,000)	Grasses, sedges
Bitterroot Basin*	46 - 47	1,677 (5,500)	(no information)
Salmon River Basin	44 - 45.2	1,677 (5,500)	Grasses, willows
Teton Valley	43.7 - 44.3	1,830 (6,000)	Grasses, willows
MONTANA			
Kalispell Basin*	48 - 49	762 (2,500)	Grasses, sedges, willows
Helena Basin*	46.5 - 47	976 (3,200)	(no information)
Crazy Mountains Basin	45.5 - 46.5	1,250 (4,100)	(no information)
WYOMING			
Wyoming Basin	42.2 - 43.1	1,616 (5,300)	Grasses, saltbush, black sage, greasewood
Red Desert Basin	41.4 - 42.3	2,043 (6,700)	Black sage, saltbush, greasewood
Wind River Basin	42.5 - 43.5	1,677 (5,500)	Grasses, western sage
Washakie Basin	41 - 41.5	1,677 (5,500)	Black sage, saltbush

Table 7. (Continued)

Intermountain basins	Latitude (degrees N)	General elevation m (ft)	Dominant species
Bridger Basin (Green River Basin)	41 - 43	2,135 (7,000)	Grasses
Great Divide Basin	41.2 - 42.5	2,135 (7,000)	Grasses, black sage
Shirley Basin	41.3 - 42.1	1,891 (6,200)	Saltbush, black sage
Laramie Basin	40.8 - 41.3	2,135 (7,000)	Grasses, black sage
Big Horn Basin	43.5 - 45.5	1,372 (4,500)	Black sage, rabbitbrush, saltbush, greasewood
Powder River Basin	42.7 - 45	1,311 (4,300)	Grasses, black sage
Jackson Hole	43.5 - 44.2	1,921 (6,300)	Western sage, grasses
COLORADO			
Gunnison Basin	38.2 - 38.6	2,135 (7,000)	Western sage, grasses, sedges, rushes
Las Animas Basin*	37.2 - 37.4	1,982 (6,500)	Grasses, sedges, rushes, willows
Middle Park	39.5 - 40.2	2,592 (8,500)	Western sage, grasses
Montrose Basin*	38 - 39	1,830 (6,000)	Saltbush, shadscale, grasses
North Park	40.3 - 41.2	2,714 (8,900)	Western sage, grasses, sedges
San Luis Valley	36.7 - 38.2	2,531 (8,300)	Greasewood, saltbush, salt grass, rabbitbrush

Table 7. (Concluded)

Intermountain basins	Latitude (degrees N)	General elevation m (ft)	Dominant species
South Park	38.6 - 39.3	2,989 (9,800)	Grasses, fringed sage
Eagle/Walcott Basin*	38.5 - 39.5	1,981 (6,500)	Saltbush, rabbitbrush, grasses, sedges, greasewood
Wet Mountain Valley	37.8 - 38.1	1,982 (6,500)	Grasses, fringed sage
Yampa Basin	39.9 - 41.4	2,135 (7,000)	Mixed shrubs, grasses
NEW MEXICO			
San Juan Basin	36.5 - 37	1,830 (6,000)	Shadscale, saltbush
Sandia Basin*	34.1 - 35.1	1,525 (5,000)	Shadscale, saltbush
Elephant Butte Basin*	32.5 - 34.1	1,464 (4,800)	Shadscale, saltbush
Tularosa Basin	32 - 35.5	1,311 (4,300)	Mesquite, Spanish bayonet
Jornada del Muerto	32.5 - 34.2	1,525 (5,000)	Shadscale, mesquite
Estancia Valley	34.5 - 35.2	1,860 (6,100)	Shadscale, mesquite

*Names given to basins that do not now have official geographic names.

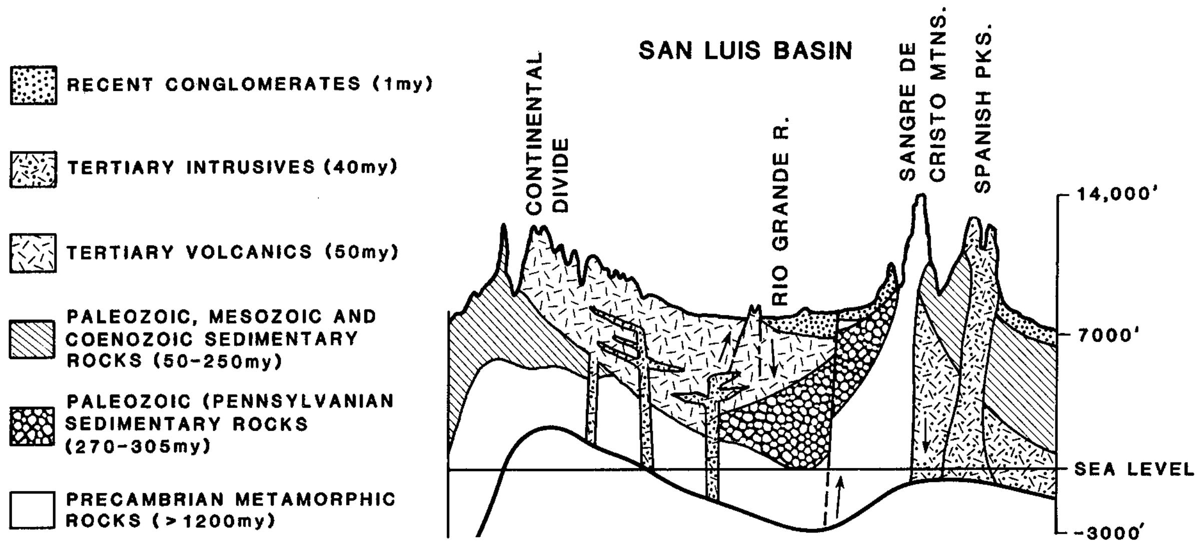


Figure 9. East-west cross-section through the central San Luis Basin (Colorado) illustrating: (1) surface configuration; (2) relationship of underlying rocks with surface profile; (3) age, nature, altitude, thickness, and distribution sequence of rock layers; and (4) location, nature, and magnitude of structural elements. (Adapted from Oetking et al. 1967.)

1.6 MAJOR CATEGORIES OF ROCKY MOUNTAIN WETLANDS

We have grouped Rocky Mountain wetland communities, for purposes of discussion in this report, into four major categories: (1) communities located in permanent shallow standing waters; (2) communities with seasonal or permanent high water tables, but without permanent standing water; (3) communities adjacent to running waters; and (4) communities located in running waters (streams, rivers, canals, and ditches). In all of these wetlands, the water table is at, near, or covering the soil surface, at least periodically. To ensure consistency with the Cowardin et al. (1979) classification system, these community types are cross referenced in detail in Chapter 3 of this report.

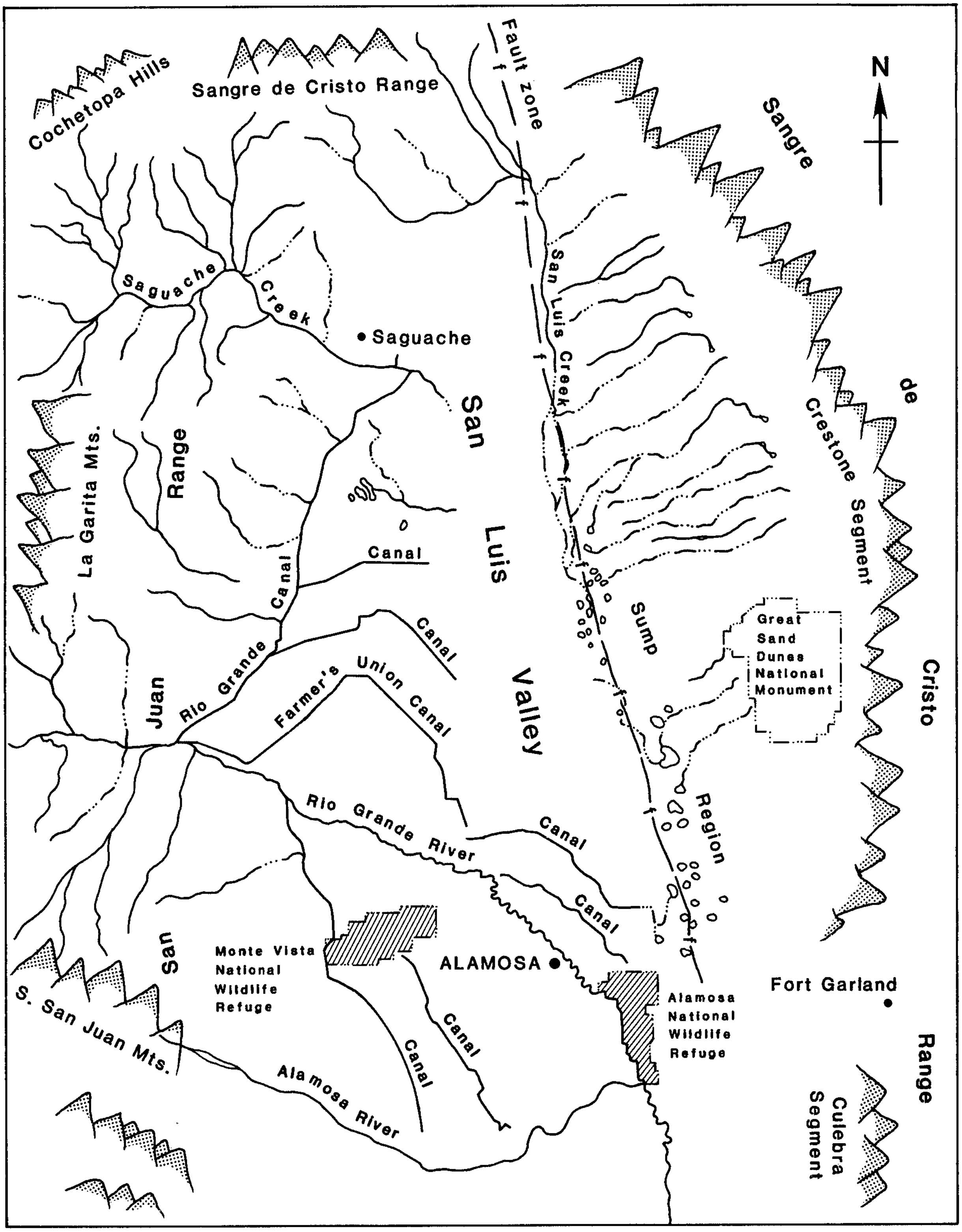


Figure 10. Northern and central San Luis Valley with surrounding mountain ranges and major drainages. (By S. Q. Foster.)

Communities Located in Permanent Shallow Standing Waters

Permanent shallow standing waters in the Rocky Mountains are of the following types: (1) beaver, oxbow, and moraine ponds; (2) kettle and semi-drainage moraine ponds; (3) cirque lakes and tarns; (4) nivation depression and solifluction terrace pools in cirques; (5) lakes and ponds in intermountain basins; and (6) those created by human activities, such as stocktanks, reservoirs, and impoundments maintained for livestock, domestic water storage, and irrigation. They may be permanent for hundreds to thousands of years, depending on their depth, basin area, substrate character, local hydrological regimes, and precipitation and evaporation rates. Their formation can result from: (1) glacial or floodplain processes, (2) alteration of drainage patterns by volcanic or tectonic movements, or (3) beaver activities and human structures.

These water bodies may have classic and relatively universal sets of life forms invading them, in a predictable sequence (hydrarch succession). However, some wetland types do not proceed through classic successional stages and may, in fact, remain permanently as wetlands. Life forms inhabiting these wetlands vary with differences in water temperature and chemistry; depth, frequency, and degree of water fluctuations; duration of cover by snow or ice; and biological history. High-elevation and newly formed lakes and ponds are oligotrophic (nutrient poor) due to low water temperature, limited dissolved organic and inorganic nutrients, and, in some cases, rapid replacement of water in the system (Figure 11A). Oligotrophic lakes tend to remain so over time, sustaining very little plankton, few submerged or floating vascular plants, and low animal populations. At lower elevations, eutrophication (gradual nutrient enrichment) may result from increased productivity of plants and animals and consequent accumulation of organic materials and nutrients (Figure 11B) (Wetzel 1983). Wetland areas that now appear to be marshes, fens, carrs, or wet meadows may have originated as lakes or ponds, which gradually passed through successional stages into their present transitional wetland state and may, in time, become upland terrestrial communities (Figure 11c).

These communities form the stages (seres) in classic developmental changes in vegetation invading open water (hydrarch succession). They have many similarities worldwide--in life forms, in processes producing changes, and in genera of plants and animals that dominate the various stages.

Communities with Seasonal or Permanent High Water Tables, but Without Permanent Standing Water

This large category is composed of wetland communities that are spatially removed from streams, but their high water tables may be maintained by periodic overbank flooding of streams; the interaction of the stream flow with the groundwater table; or by sources of water other than streams (e.g., lakes, springs). The water is usually considerably lower in oxygen than any of the other three types. Most fens, carrs, wet meadows, and shrub wetlands are in this category. Some factors that affect the character of these wetlands are type and proximity of bedrock topography; climatological effects associated with elevation, latitude, and longitude; levels and stability of the water table; soil nature, composition, and depth; solar exposure; and biological and ecological history.

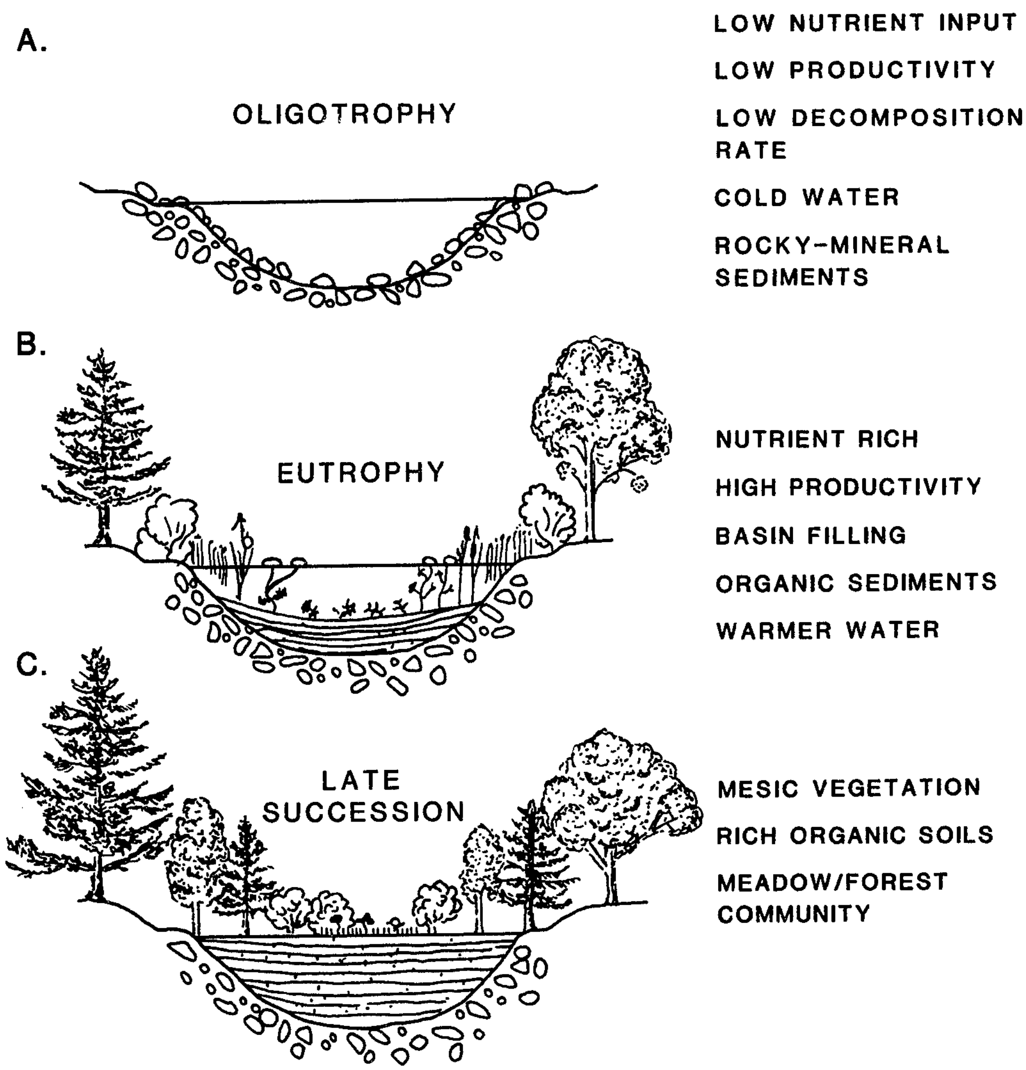


Figure 11. Changes in a lake basin over time. Seral stages: (A) a new lake is oligotrophic (nutrient poor); (B) as nutrients and productivity increase, it becomes eutrophic; and (C) in time, a lake may fill in and become a meadow or a forested area. (By S. Q. Foster.)

In the Rocky Mountains, there are four major types of these communities, based on life form of the dominant plants: (1) herb wetlands, (2) shrub wetlands, (3) forested wetlands, and (4) unvegetated wetlands. Each of these major types has several specific ecosystems within it; each of which reflects differences in dominant plants, nature of substrate (organic or mineral), chemistry, and source of water. There is much more diversity of ecosystems within this group than within either of the other major wetland categories.

Communities Adjacent to Running Waters

Wetland communities in this category occur riparian zones. These wetlands tend to be created and maintained by a high water table adjacent to and connected with streams. They are flooded very frequently as the stream exceeds channel capacity. These communities experience high oxygenation of water and

receive considerable spray in some sites. In the West, riparian communities are very characteristic of waterways; in drier parts of the Rocky Mountains, riparian communities stand out in sharp contrast to surrounding ecosystems by the luxuriance of their vegetation and the variety of animal species that are found there as permanent residents or transients. Riparian communities have a considerable effect on fertility and productivity of the adjacent stream waters.

Communities Located in Running Waters

This category of Rocky Mountain wetlands includes those communities within active stream channels that either periodically or continuously contain moving water. They are the equivalent of the Riverine System as described by Cowardin et al. (1979). They begin as headwater streams, and for purposes of this report, end at the lower limit of the Lower Montane Life Zone or in intermountain basins. Springs, and sometime seeps, may be extensions of these community types. They are bounded on the landward side by the riparian zone, riparian wetlands, or wetland communities adjacent to running waters. Inflow water, runoff water, and subsurface (ground) water controls to a great extent the amount of flow within these wetland communities.

Most major streams originate in alpine basins and are fed by direct precipitation, melting snowbeds, and glaciers. Peak discharge of water carried by these streams occurs in late June and early July, due to snowmelt at the headwaters (Figure 12). Frequency and severity of flooding is a function of peak runoff amplified by magnitude of annual snowpack accumulation, rapidity of melting, intensity and duration of precipitation events, steepness of slope, and amount of uptake by soils. The severity and duration of flooding controls the areal extent, depth, proximity, and wetness of upstream wetlands (Novitzki 1979; Jarrett and Costa 1984).

In places of steep gradient, streams flow at high velocities over bedrock waterfalls and over boulders and rubble, creating cascades. Rapids and riffles are interspersed with turbulent pools and quiet water reaches. Such streams are powerful erosional forces, rolling boulders and other loose substrate downstream and, at the same time, entrenching themselves into deep stream channels by means of the combined cutting action of water and transported materials. Dislodged sand, mud, clay, and organic matter create turbid conditions when suspended in water in high concentrations.

As stream gradients decrease, some suspended materials and bed loads are deposited. The ultimate expression of reduced gradient occurs in intermountain basins and in wide, glacial mountain valleys where lakes have been filled and streams meander across the flat alluvium of the filled lake or intermountain basin. Such streams migrate back and forth across the floodplain over a period of years (Leopold and Langbein 1966). Very sharp meander bends may be cut off by flood waters that breach the narrow neck of land between upstream and downstream channels, creating a new, more linear, stream channel

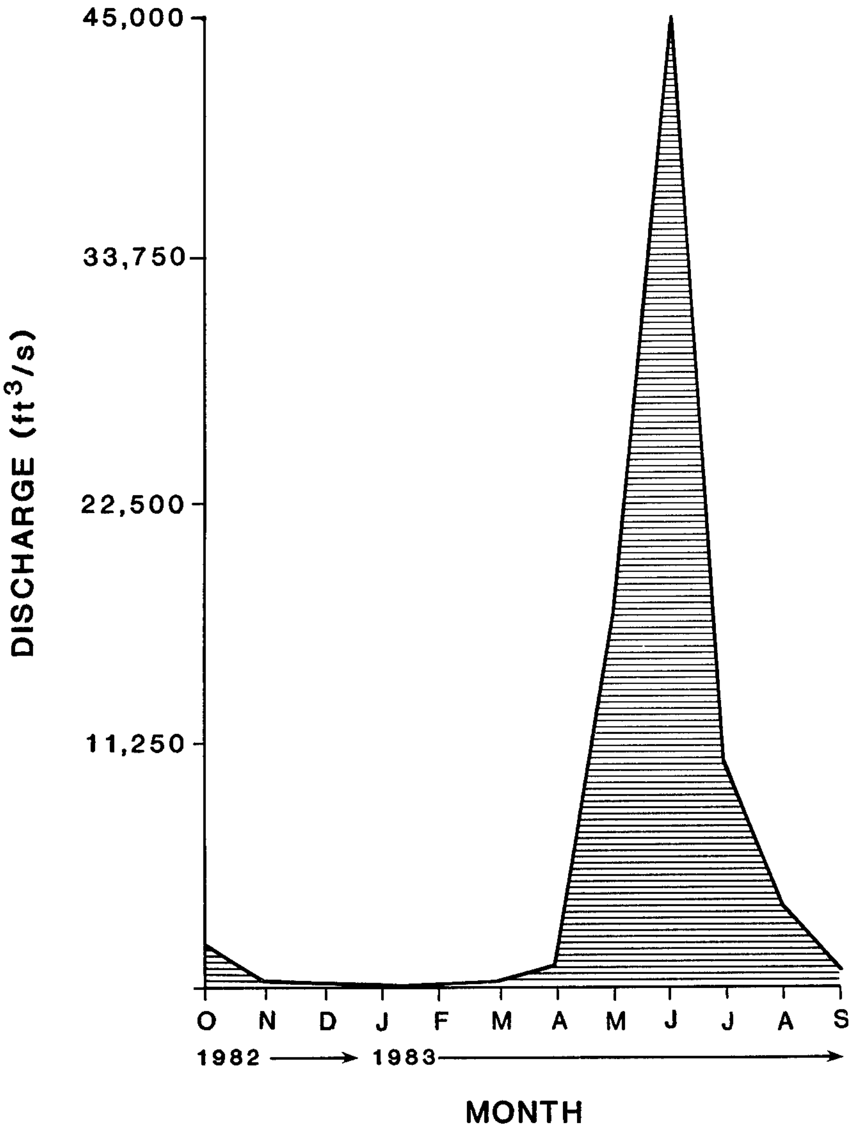


Figure 12. Mean monthly discharges from Big Thompson River at Loveland, Colorado, for water year October 1982 to September 1983. (From U.S. Geological Survey 1983.)

(Figure 13). The abandoned stream meander or "oxbow" remains as a small wetland adjacent to the stream channel (wetland category 2). It commonly becomes inundated and scoured during peak annual runoff. During these flood periods, water erodes stream banks and scours substrates in the main channels, removing organic matter, submergent, emergent, and pioneering terrestrial plants and bottom-dwelling animals established during earlier periods of low flow.

Diversity and productivity of plant and animal life in running water wetland communities depend on: (1) water velocity; (2) frequency and severity of flood and anchor ice scouring; (3) substrate character and stability; (4) water temperature; (5) pH, alkalinity, hardness, and concentrations of dissolved nutrients; (6) amounts, sizes, and composition of suspended and

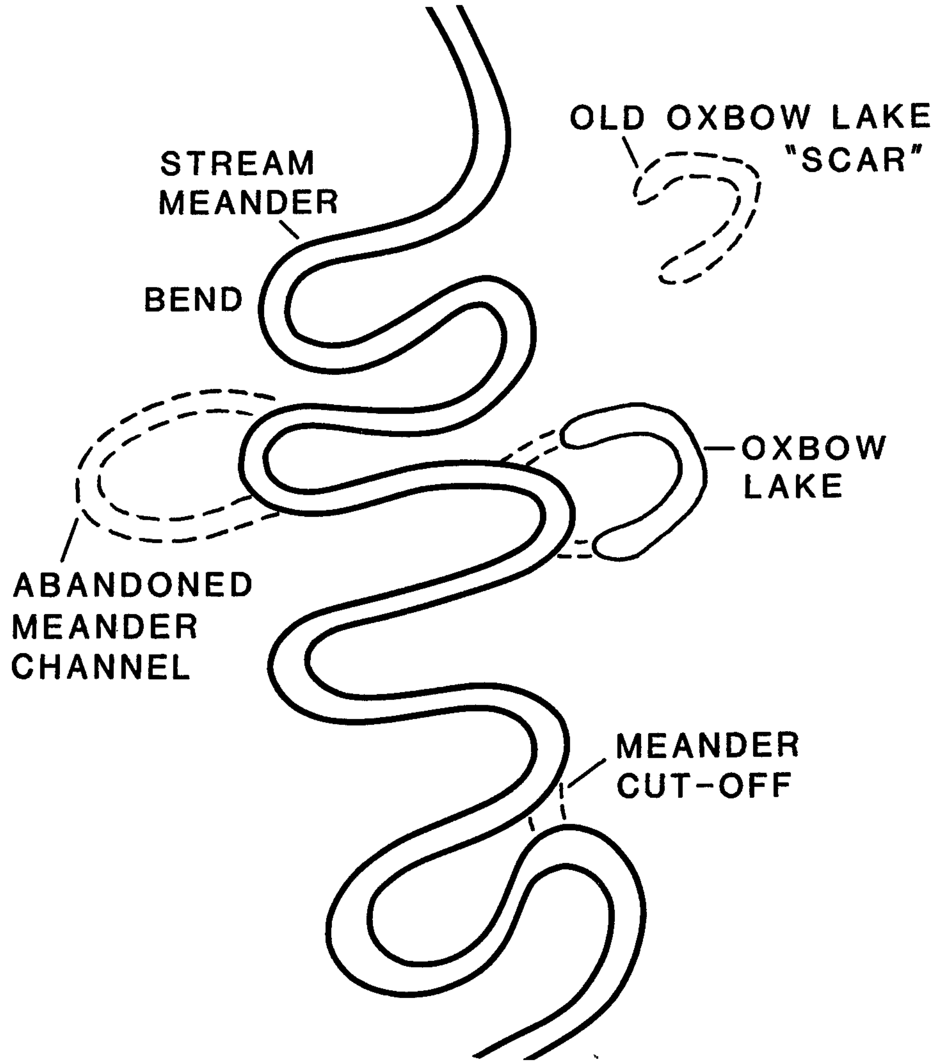


Figure 13. Features associated with a meandering river and its floodplain, including meander bends, cut-offs, abandoned channels, oxbow lakes, and old oxbow lake scars. (By S. Q. Foster.)

deposited organic particles from land and stream organisms; (7) physical, chemical, and biological influences of stream bank (riparian) vegetation; and (8) hydrological processes shared with neighboring wetlands (Hynes 1970).

Headwater streams (stream orders 1, 2, and 3) are generally low in species richness, diversity, and productivity, due to cold water temperatures and very low dissolved nutrient content of the water (Winget and Mangum 1979). Most of their organic material comes from adjacent riparian ecosystems (Likens and Borman 1974). As with streams in other parts of North America, diversity, richness, and productivity increase with distance from headwaters (Mathis 1967; Harrel and Dorris 1968; Cook 1976).

The role of beaver in obstructing and diverting running waters and making dry areas into ponds and wetlands is well known and characteristic of mountain valleys throughout the Rocky Mountains. We point out this relationship and describe beaver activity in damming running waters; however, the wetland communities produced by beaver activities are included under wetland category 2 in Chapter 3.

Alteration of running waters and creation of wetlands by the American beaver (Castor canadensis) cannot be underestimated. By damming small streams with woody material, beaver create pond and lake habitat in which they build lodges and store food for winter (Figure 14). Given adequate woody plant species for food and building materials, beaver may be found up to 3,200 m (10,500 ft) in elevation. Aspen and cottonwood are preferred foods; however, willow is extensively utilized in the absence of larger trees. When food resources are exhausted or when the pond or lake becomes too silted-in and shallow to allow winter travel under ice, beaver move up- or downstream in search of new habitat. Young beaver seek new habitat and create new wetlands when driven from their parents' territory. Beaver ponds are colonized by diverse species of invertebrates, an important food source for brooding ducks, ducklings, and fishes. Complex wetland plant communities provide food, shelter, and cover for many other wildlife species. Abandoned beaver ponds pass through wetland seral stages, becoming a fen and eventually a willow/shrub wetland or a forest (Grasse 1951; Arner 1963; Brayton 1983).

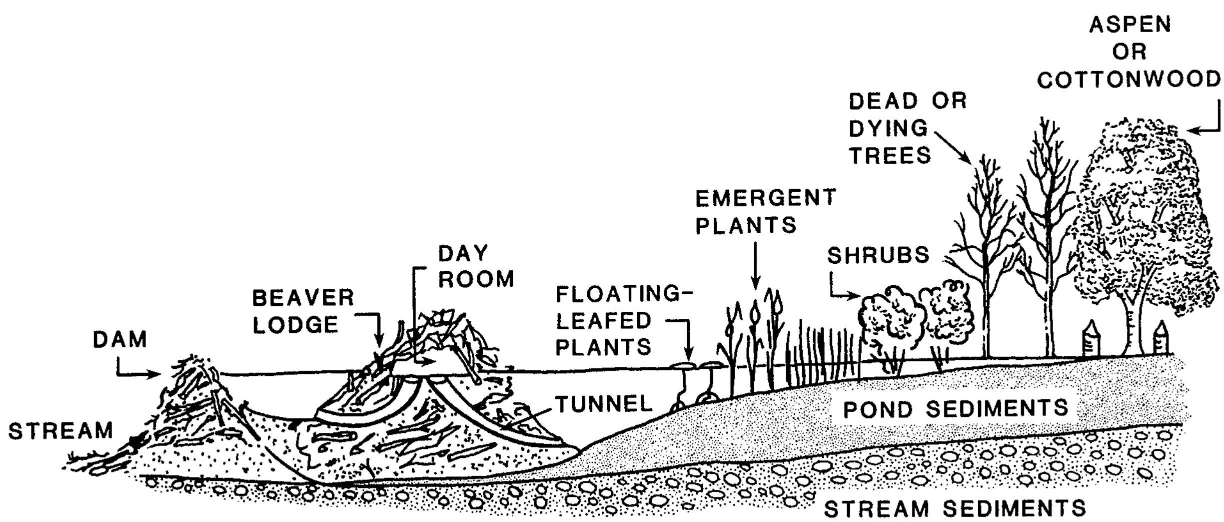


Figure 14. Beavers dam streams and create pond and lake habitat (wetlands) in which they build lodges and store food for the winter. Beaver ponds pass through typical hydric seral stages. (By S. Q. Foster.)

CHAPTER 2

GEOLOGY, HYDROLOGY, CLIMATE, AND SOILS OF THE ROCKY MOUNTAINS[1]

2.1 ORIGIN AND STRUCTURE OF THE ROCKY MOUNTAINS

The Rocky Mountains are relatively young mountains that owe their existence to the large-scale forces associated with plate tectonics (continental drift).

Mountain-building processes are believed to result from the collision of tectonic plates as they slide over the partially molten mantle of the earth's interior. According to plate tectonic theory, 400 million years ago, North America, Eurasia, and Africa were joined as one large continent. The Atlantic Ocean was formed as the North American plate began to separate and drift west, a process that continues today. As the North American plate collides with the Pacific plate to its west, lateral compression causes folding, faulting, earthquakes, and volcanism along the two plate boundaries. The Rocky Mountains are one result of this compression process, which is taking place along the eastern Pacific rim from Alaska to the southern end of South America (Wilson 1970).

Radiocarbon and potassium-argon dating of rock materials have been used to approximate relative ages of formations, relating their history to the geologic time scale. Four eras of geologic history are identified: Pre-Cambrian, Paleozoic, Mesozoic, and Cenozoic (Table 8) (Atwood 1945; Eicher 1976).

<u>Pre-Cambrian Era</u> (2.3 billion to 600 million years before the present [BP])

During late Pre-Cambrian time, sandstones, shale, and limestone accumulated in a large geosyncline, expanding throughout western North America, which sank 4,575 m (15,000 ft) to 15,250 m (50,000 ft) as sediment accumulated (Haun and Kent 1965).

<u>Paleozoic Era</u> (600 million to 240 million years BP)

Gentle deformation and pressure, increasing with sediment accumulation, was sufficient to alter the sediments into some granites and some gneisses and schists. Evidence of brief intervals of marine invasion alternating with periods of erosion is found in Ordovician, Silurian, and early Devonian rocks.

[1]Authored by L. P. Rink and G. N. Kiladis.

Table 8. Geologic calendar for the Rocky Mountain region. (Modified from Atwood 1945.)

Era	Period	Epochs	Rock materials	Chief events
Cenozoic 65 million years before the present (BP) to the present	Quaternary	Post-glacial Neo-glacial (Little Ice Age) Hypsithermal	Stream deposits Sand dunes Peat in bogs and swamps	Vigorous stream action Glaciers shrinking Winds active Mountain growth continues
		Pleistocene (The Great Ice Age)	Glacial moraines Sand and gravel deposits Stream deposits	Alpine glaciers in all high mountains Moraines deposited Lake basins formed Ice-front lakes All streams flooded Mountain growth continues
	Tertiary	Pliocene	Vast amounts of stream deposits Volcanic outpourings	Great mountain growth Peneplantation of large areas Widespread filling of basins
		Miocene	Stream deposits Lake deposits Volcanic materials	Mountains being worn down Volcanic eruptions
		Oligocene	Stream deposits Lake deposits Volcanic materials	Mountains being worn down Volcanic eruptions
		Eocene	Stream deposits	Active erosion in mountains
		Paleocene	Glacial moraines	Glaciation in mountains Mountain growth continuing
Mesozoic 240 million to 60 million years BP	Upper Cretaceous		Mesa Verde sandstone, a wide-spread mesa-capping Dakota sandstone, a great hogback maker Shales, conglomerates, coal	Great mountain growth Birth of Rocky Mountains Volcanic activity
	Lower Cretaceous		Sandstones, shales, conglomerates, limestones	Periods of sedimentation in the Rocky Mountain Region
	Jurassic		Sandstones, shales, conglomerates	
	Triassic		Red sandstones, red shales, conglomerates	

Table 8. (Concluded)

Era	Period	Epochs	Rock materials	Chief events
	Permian		The lower or older Red Beds	Making of many of the Red Beds
<u>Paleozoic</u> 600 million to 200 million years BP	Mississippian Pennsylvanian Devonian Silurian Ordovician Cambrian		Represented in Rocky Mountains by limestones, shales, sandstones, conglomerates	In general, a long period of sedimentation in the Rocky Mountain region. The ocean waters invade this area several times. Areas of accumulation shift Some crustal movements
<u>Pre-Cambrian</u> In Rocky Mountains, 2.3 billion years to 600 million years BP			The fundamental or Pre-Cambrian complex The core rocks in many of the mountain ranges Rocks include: schists gneisses quartzites slates Granitic intrusions: many dark intrusives some little altered sedimentary formations	During this very long era there were several mountain-making periods, great vulcanism, long periods of erosion, and, at some places in the world, glaciation. A complex history, never to be worked out in detail.

One major invasion of a sea is recorded in sediments dated to the Devonian/Mississippian Period (Haun and Kent 1965). Significant tectonic activity in the form of gradual uplift occurred during the Pennsylvanian and Permian Periods to create the "ancestral Rockies." Their elevation fluctuated between 0 and 610 m (2,000 ft) and took place during uplift events (Harris 1975).

Mesozoic Era (240 million to 60 million years BP)

These Paleozoic beds were eroded away from uplifted surfaces during the Mesozoic Era, supplying adjacent basins with sandstone, carbonates, evaporites, and coarse clastic sediments. Swampy regions prevailed in tropical climate, accumulating peat, which later turned to coal. A vast boreal sea extended from the Arctic into the northwestern and western parts of the region by the late Jurassic (Haun and Kent 1965). By 100 million years BP, seas inundated the entire region (Harris 1975).

Cenozoic Era (Tertiary and Quaternary) (65 million years BP to present)

The present tectonic framework of the Rocky Mountains evolved during the late Cretaceous and early Tertiary. Uplifting of mountains and depression of intermountain basins, involving both folding and faulting processes, developed in what is known as the Laramide Orogeny, which began approximately 70 million years BP in late Cretaceous time and started at slightly different times in different places within the Rocky Mountain Province. The mountains rose some 1,525 m (5,000 ft) about 60 million years BP. Rapid uplift resulted in faulting, which in turn triggered volcanic activity. Faulting occurs when the crust cracks and slides laterally or vertically relative to its original position. Vertical faults either elevated or lowered beds (Figure 15). Thrust faulting forced older beds over younger ones. Dikes invaded faults during Tertiary time, forcing fluids rich in gold, silver, lead, and zinc through the fractured rock. Movements induced by faulting can be responsible for large intermountain basins or steep ranges, such as the Grand Tetons (Figure 15).

Pre-Cambrian and younger sedimentary beds were exposed as faulting and folding took place. Metamorphic Pre-Cambrian rocks, dated at 2.6 billion years BP, are found in the Medicine Bow Range in Wyoming; metamorphic rocks, dated 1.74 billion years BP, have been found in the Front Range of Colorado. Folding created anticlines and synclines commonly expressed in the landscape as ridges and valleys (Figure 16). Most of the eastern ranges in the southern and central Rocky Mountains were formed primarily by folding processes. Along the eastern and western margins of the southern Rocky Mountains, the overlying deposits are visible today in places as steeply dipping "hogbacks" and "flatirons" of sedimentary rock (Figure 16). The present angle of these formerly flat surfaces attests to the large scale folding that took place as the Rocky Mountains were formed (Atwood 1945).

During the Laramide Orogeny, 4,575 m (15,000 ft) to 13,725 m (45,000 ft) of structural relief developed. Erosive forces acted to reduce elevation while some basins experienced more than 4,880 m (16,000 ft) of sedimentation (Haun and Kent 1965). Erosional surfaces developed through the region, later to be uplifted.

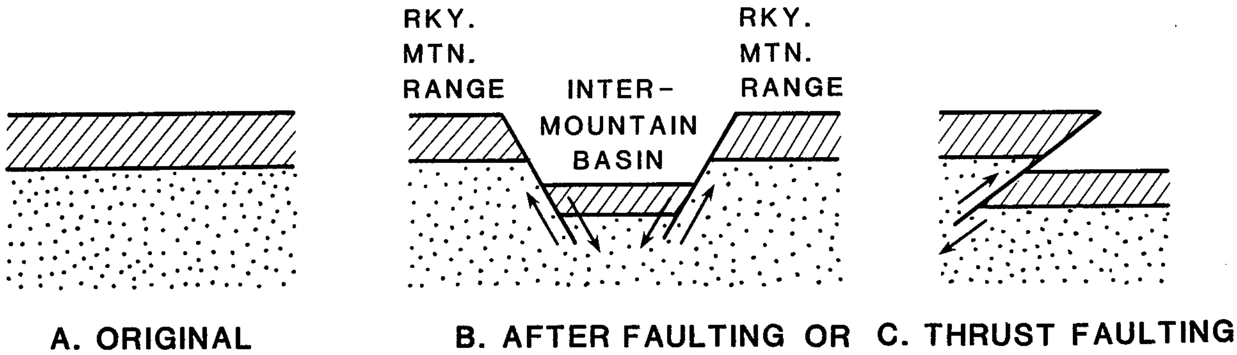


Figure 15. Vertical faults occur when the Earth's crust is compressed by two plates pushing against each other causing vertical cracks and slides relative to the original position. (By L. P. Rink.)

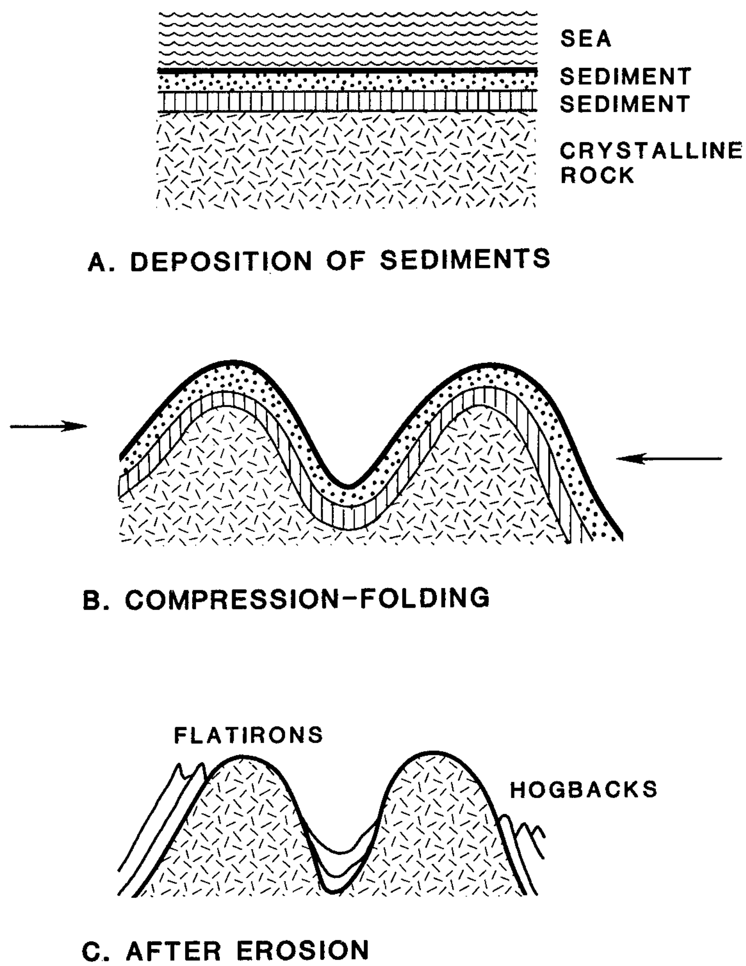


Figure 16. Folding is caused by warping of the Earth's crust as it is squeezed or extended laterally by plate tectonic movements. (By L. P. Rink.)

Post-Laramide tectonic activity involved regional uplift and normal faulting. Many of the present geomorphic features (basins and mountain ranges) are related not to the Laramide Orogeny but to later Cenozoic uplift, volcanism, block faulting, and erosion.

2.2 LANDFORMS, EROSION/DEPOSITION PROCESSES, AND WETLAND CREATION

Erosional and Depositional Processes

Water is the primary erosional agent producing the landforms of the Rocky Mountains. The landscape has been reshaped by precipitation, surface flow, subsurface flow, freeze/thaw action, and movement of glacial ice (Thornbury 1965). Erosion occurs relatively quickly given the steep gradients of the mountain ranges, carving steep sided, narrow V-shaped valleys in the lower mountains. Water-born sediments have accumulated in the intermountain basins to thicknesses in excess of 4,880 m (16,000 ft) (Haun and Kent 1965).

One major result of water erosion is expressed today in remnants of large, conspicuous high-elevation erosion surfaces (Thornbury 1965). The latest research indicates that a period of stability in the late Eocene, lasting about 3 million years (Epis and Chapin 1975), allowed a large regional erosion surface to form in the southern and central Rocky Mountains. Differential uplifting and faulting of this surface during the Miocene and Pliocene created the gently rolling ridgetops so characteristic of today's mountains. This period of structural building completed the formation of the modern ranges and intermountain basins. However, much of the rugged high mountain terrain seen today is the result of former glacial activity.

Per unit area, glaciers are the most effective erosional agent (Thornbury 1965). Their direct influence on Rocky Mountain landscape has been restricted to the high mountain valleys, except where glaciers originating in Montana mountains reached the Great Plains just south of the Canada border (Figure 17) (Flint 1971; Price 1981). At present, glaciers are limited in extent in the Rocky Mountains of the United States (Figure 18).

Pleistocene mountain glaciation began in the Rocky Mountains about 1.5 million years ago. Evidence of several major glacial periods is found in most of the ranges of the Rocky Mountains (Wright 1983). The estimated ages and duration of these periods change frequently as more field research is done on glacial deposits and pollen rains in lakes and marshes. Glacial sculpturing and resulting deposits were a major factor in creating the wide variety of sites for wetlands in the Rocky Mountains (see section 1.5).

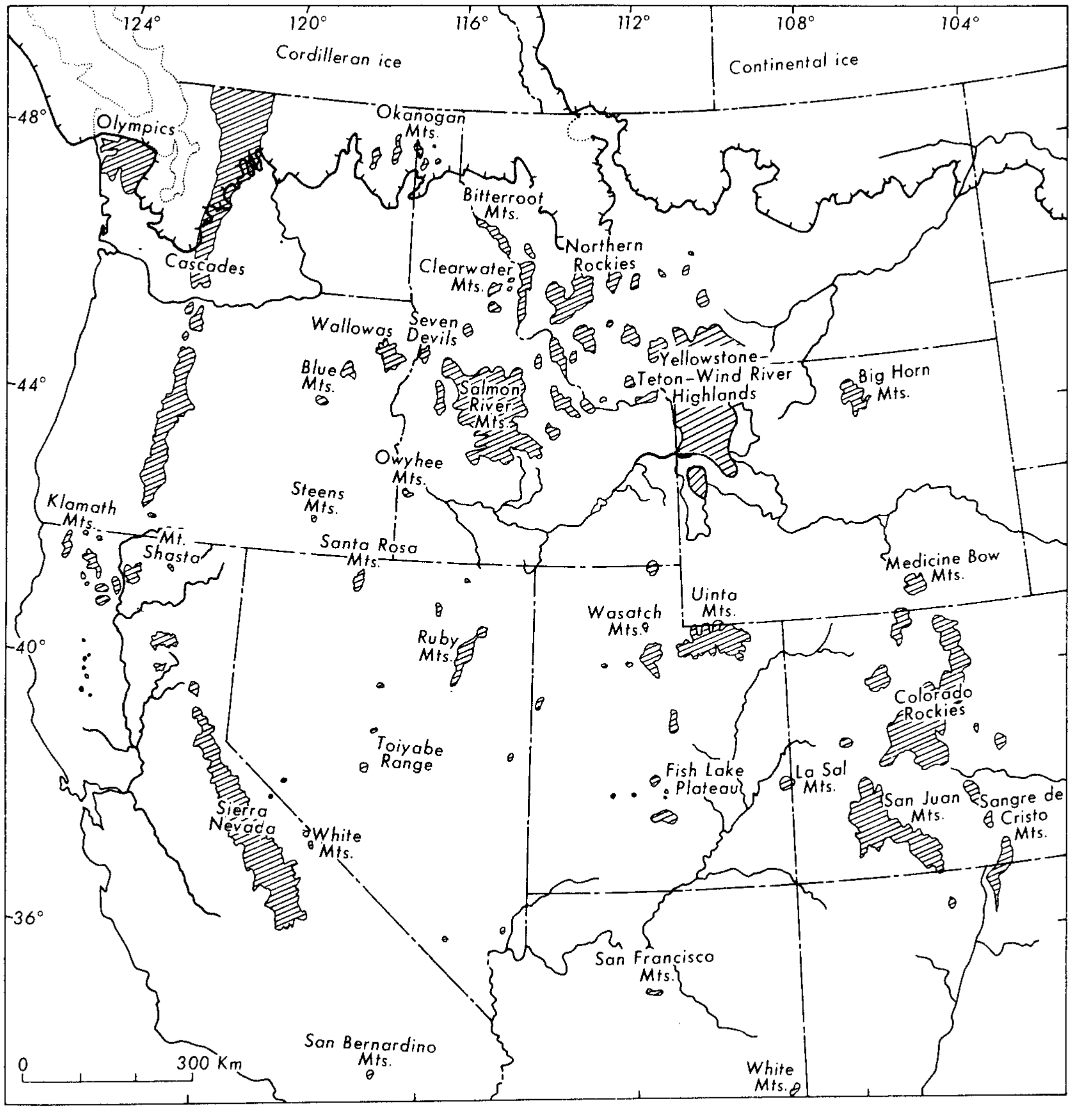


Figure 17. Generalized extent of mountain glaciation during the Pleistocene. (From Price 1981, which was adapted from Flint 1971 and U.S.G.S. 1970.) Note that part of the northern Rockies in Montana and Idaho are within the area of continental glaciers; in this area mountain glaciers fused with continental glaciers at lower elevations.

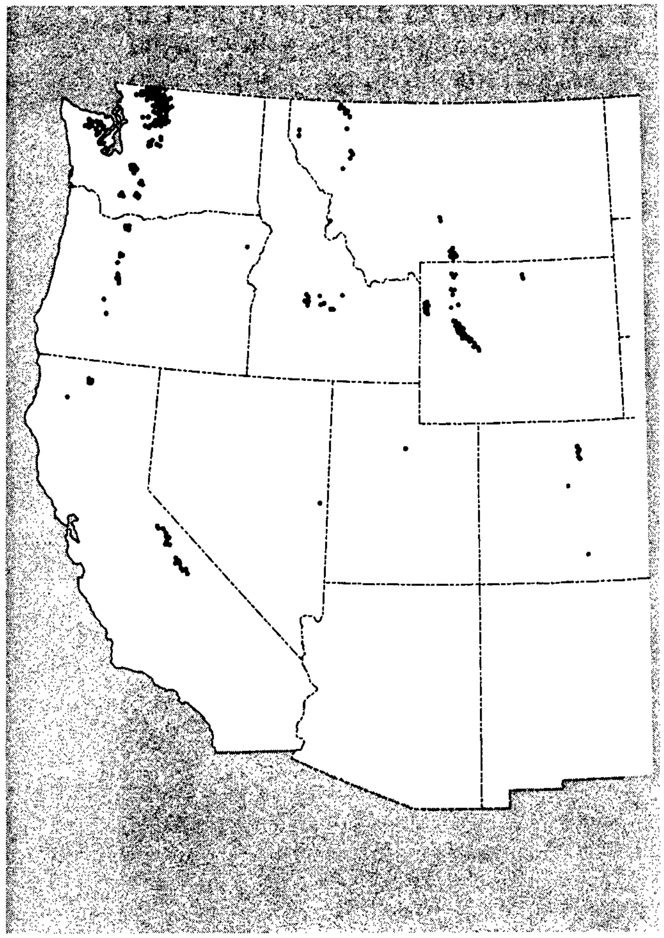
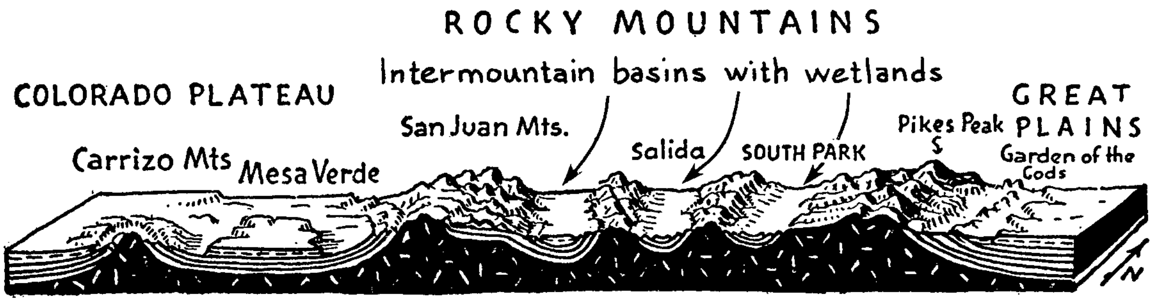


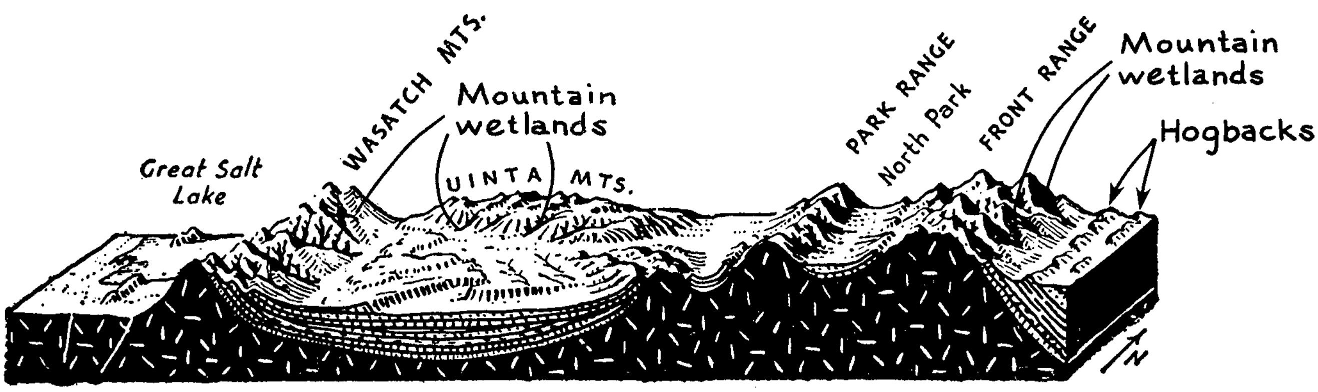
Figure 18. Current extent of glaciers in the western United States. (From U.S. Department of the Interior, Geological Survey 1973.)

Landforms and Wetland Creation

Landforms of the Rocky Mountains are characterized by four major features: (1) individual ranges separated by large intermountain basins; (2) extensive, large, gently rolling surfaces of the mountain and ridge summits; (3) characteristic water-produced features in lower reaches of valleys; and (4) typical mountain glacial features in upper reaches of valleys. Type and rate of mountain building, parent material, and specific erosional processes are all important factors that have interacted to produce these characteristic Rocky Mountain landforms. Typical cross-sections spanning many landforms of varying geological composition across a number of latitudes in the Rocky Mountains are shown in Figure 19A-F; it is indicated on each where wetlands may be found. Descriptions of location of wetlands and processes producing the sites are given in section 1.5.

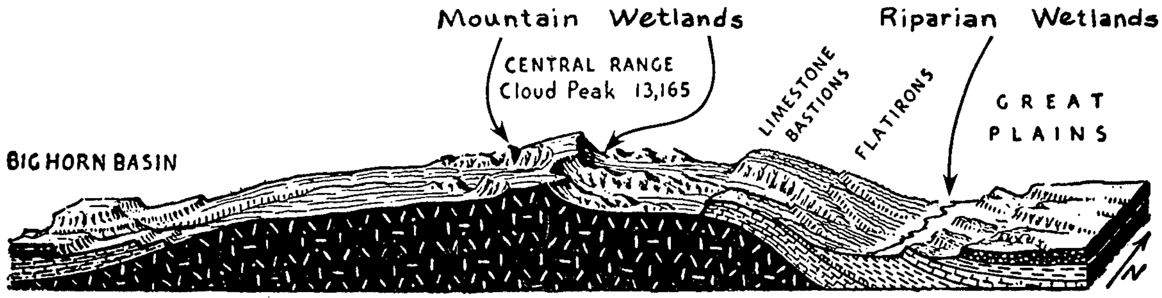


A
At the Garden of the Gods in southern Colorado, surface rocks are upturned, standing on edge. At Pikes Peak and in the Front Range, the core-rocks, chiefly granite, appear at the surface and produce a picturesque landscape. Between Pikes Peak and the great dome of the San Juan Mountains are a series of lowland parks and parallel mountain ranges. These intermountain basins contain numerous wetlands. West of the San Juans, layers of rock are turned up nearly on edge again. In the Mesa Verde, home of the cliff dwellers, layers of rock are nearly horizontal. In the Carrizo Mountains is an inactive volcano.

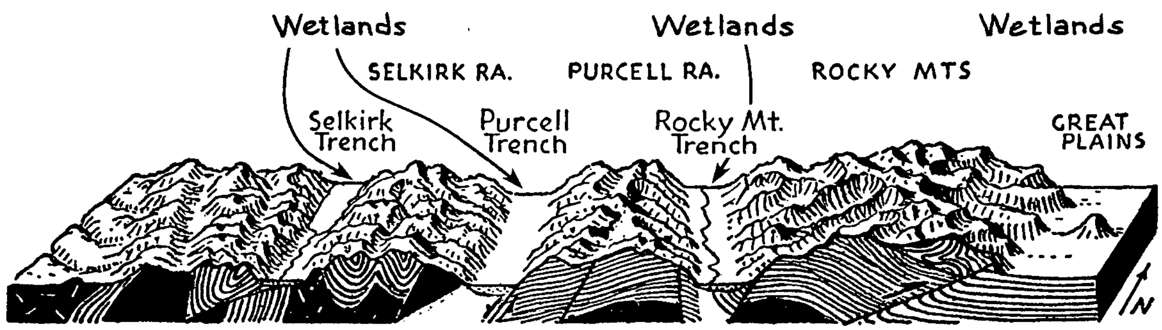


B
Cross-section of the Rocky Mountain area near the northern border of Colorado in the foothill belt east of the Front Range, where formations are upturned into hogback ridges. The Front Range stands up conspicuously with core-rocks of the ancient complex. North Park is a basin being filled with waste material washed from the mountains and contains many wetlands. West of the Park Range are the Uinta Mountains, which extend east-west. Although it does not show in the drawing, the Uinta Range is a hugh anticline. The Wasatch Mountain Range is a great fault block; it rose above the general level of the country, during a late mountain-making period along a fracture plain shown at the west base of the range. The Great Salt Lake, at its base, is surrounded by many wetlands.

Figure 19. Structure sections of the southern Rocky Mountains. (After Atwood 1945.)

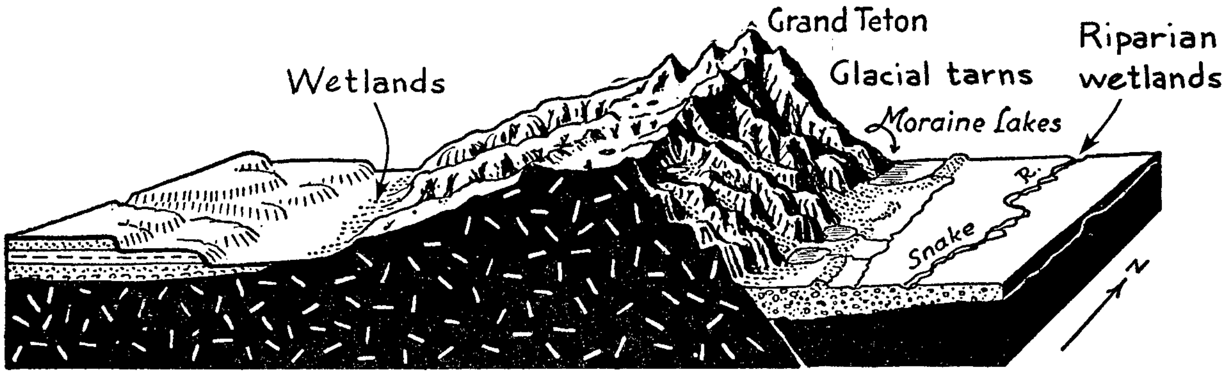


C
The Big Horn Range of north central Wyoming is a great anticlinal fold. The layers of sedimentary rock that appear to the east and to the west formerly covered the top of the range. They were removed by stream and glacial erosion. In the heart of the range, the core-rocks now appear at various places. If all the rock material removed from this great fold were replaced, the summit of the arch would be at least 10,000 feet higher than the present crest-line of the range (at 22,000 ft elevation). The streams between the Great Plains and the Flatirons are bordered by riparian wetlands.

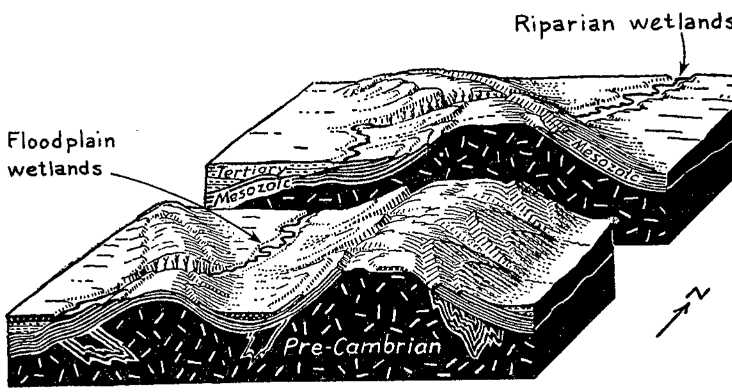


D
At the international boundary line between the United States and Canada, the structure of the Rocky Mountains is exceedingly complex. On the east are the Great Plains with horizontal sediments. Then, the Rocky Mountain Front Range, which was moved eastward by thrust faulting, rises abruptly several thousand feet into the air. To its west is the Rocky Mountain trench, where faulting caused a portion of the earth to collapse. In the ranges to the west, the rocks are very much folded, contorted, and faulted. There is one range and one trench after another. One of the long trenches contains Flathead Lake of Montana.

Figure 19. (Continued)



E
The Tetons, which have been set aside as a National park in the northwestern part of Wyoming, are carved out of a huge block of the Earth's crust that has been thrust upwards at least 7,000 feet. The fault along which this movement took place is at the east base of the range. The sedimentary rocks to the west of the range formerly extended over the summit. These sediments have been removed by weathering and erosion. Glaciers formed in this range and descended to the east basin, leaving moraines that formed the modern lakes. Floodplain wetlands are common along the Snake River.



F
Drawing of north-central Wyoming, showing where the Big Horn River cut a deep gorge through a small anticlinal mountain range at the left, then proceeded northward along the west base of the Big Horn Range, then changed course and turned directly eastward, cutting through the Big Horn Mountains. To do this, the river must have been located on a surface now washed away, which was high above these two mountain ranges. As the stream lowered its course below its former location, it cut directly across two buried mountain ranges. It is a superimposed stream. Almost all the magnificent gorges in the Rocky Mountains have been cut by superimposed streams. The Big Horn River has a border of riparian wetlands. Similar superimposed rivers have incised into ancient mountain ranges buried by younger rocks to form spectacular canyons on the North Platte River in south-central Wyoming and on the Gunnison River in central Colorado.

Figure 19. (Concluded)

High mountain valleys mark sites where glaciers dominated the landscape during the Pleistocene. Individual glaciers were small (<15 km long), but large glacier complexes formed in the San Juans and Front Range of Colorado; Wind River, Tetons, and Yellowstone Plateau of Wyoming; Uintas of Utah; and mountains in northwest Montana and central Idaho (Wright 1983). Glaciers form where snow accumulation exceeds snowmelt (Figure 20). Meier et al. (1961) report that the elevation of equilibrium lines of cirques, reflecting climatic trends, is approximately 3,700 m (12,140 ft) in Colorado and 2,500 m (8,202 ft) in northwest Montana. Most of the summits and high mountain ridges in the southern and central Rocky Mountains did not have glaciers, because they were swept clear of snow by wind.

As mountain glaciers flowed downhill they merged to form valley glaciers, often with several tributaries (Figure 21). Their powerful erosive action cut the steep-walled and flat-floored U-shaped valleys so common in mid-elevations of Rocky Mountain valleys (Thornbury 1965).

Eroded material, transported down-valley by glaciers, was deposited along the sides of glaciers, between glaciers, and at their lower ends, forming moraines. Today, these moraines form major ridges, and fill valleys. In the southern Rocky Mountains, end moraines are found down to about 2,500 m (8,200 ft); whereas in Montana, they are found as low as 1,200 m (4,000 ft) along the western portion of the Great Plains, indicative of the much greater extent of former glaciation in the northern Rockies (Richmond 1960). In Wyoming, glaciers reached into the margins of intermountain basins, where their moraines dammed drainges to form the large lakes and wetlands characteristics of the Wind River and Teton Ranges (Table 3) (Richmond 1960). Glaciers also extended into intermountain basins along the east base of the Sawatch Range and along the west base of the Sangre de Cristo Mountains (McCalpin 1981). The effect of these glacial movements where wetlands are found is described in section 1.5.

2.3 CLIMATE AND WEATHER OF THE ROCKY MOUNTAINS

It is difficult to generalize about climate and weather in the Rocky Mountains, because of the characteristically rapid changes that occur over relatively short distances. Atmospheric changes are much more abrupt in the vertical than in the horizontal. For example, the decrease in temperature due to an increase in elevation of a few hundred meters in the mountains is equivalent to going northward several hundred kilometers on the plains. To illustrate, the mean annual temperature in Boulder, Colorado, 40 °N latitude and 1,600 m (5,250 ft) elevation, is 10 °C (50 °F). Approximately 32 km (20 mi) due west at a University of Colorado weather station, 40 °N latitude and 3,700 m (12,140 ft) elevation, the mean annual temperature is -4 °C (25 °F) equivalent to that of Nome, Alaska, which is at 65 °N latitude (Barry 1973). In this case, an elevational difference of 2,100 m (6,890 ft) is equivalent to a 25-degree difference in latitude. In mountains, an increase in elevation is generally associated with a decrease in temperature. Mountain valleys, however, experience the effects of cold air drainage, where cold, dense air

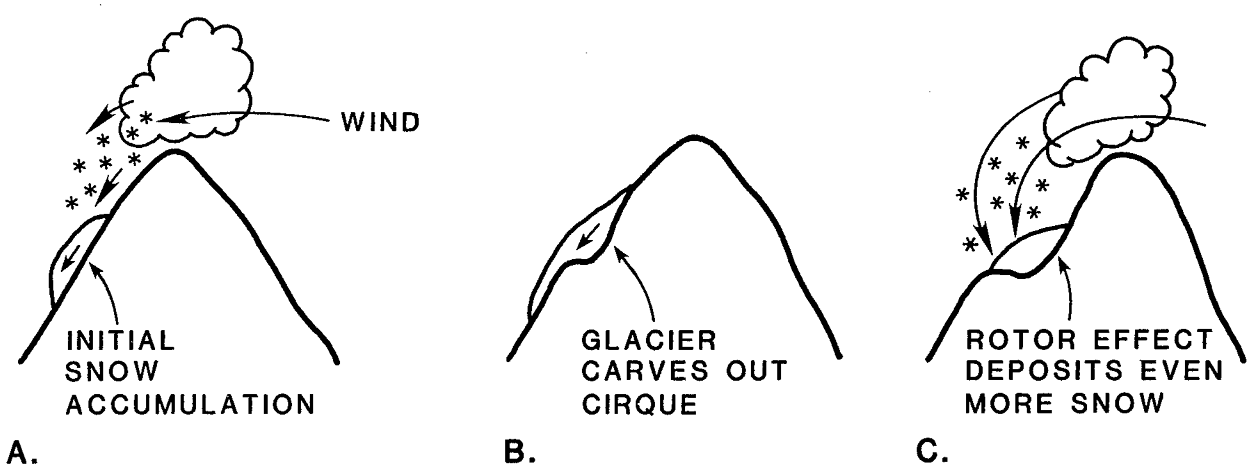


Figure 20. Cirques are formed when glaciers carve bowl-shaped depressions high on the sides of mountains. (By L. P. Rink.)

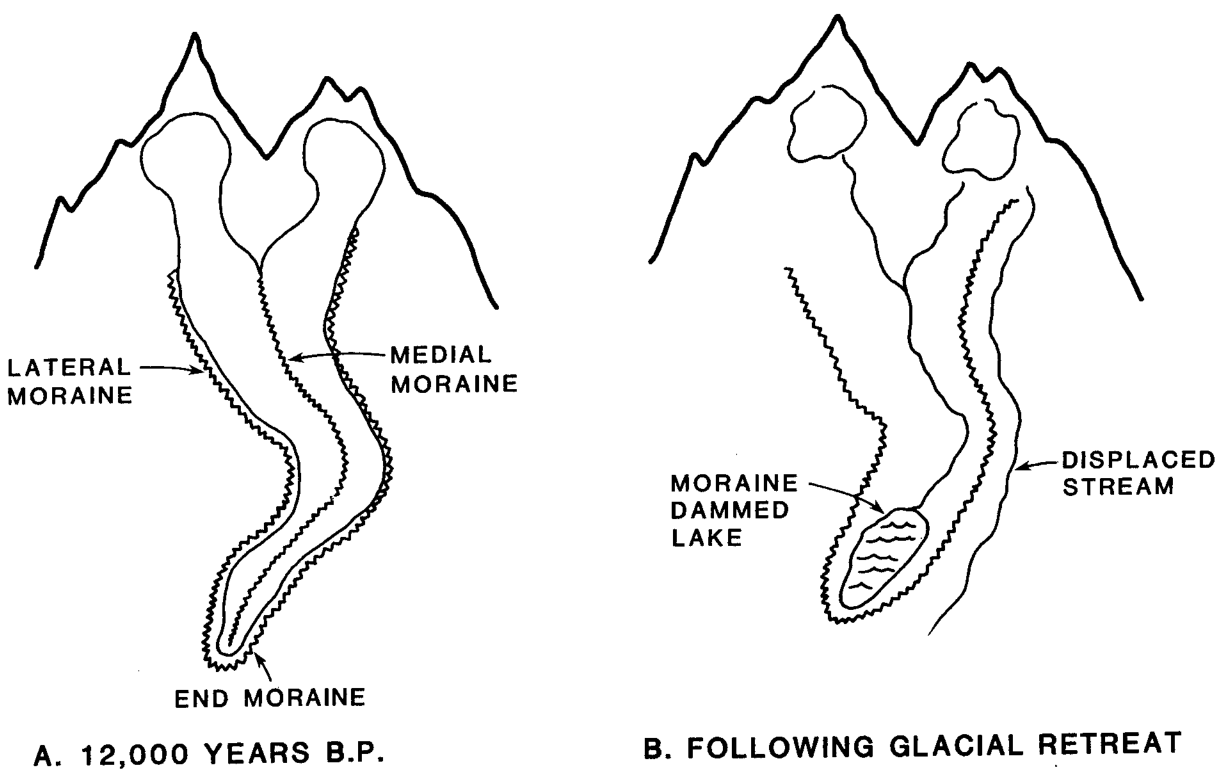


Figure 21. Many montane wetlands are the result of glacial landforms. (By L. P. Rink.)

near the surface flows downhill and accumulates in valleys (Figure 22). This results in inversions where temperature actually increases with elevation (Barry 1981). Temperature inversions occur most commonly on clear, calm nights and can be responsible for severe cold at relatively low elevations (Barry 1981). In the Rocky Mountains, the intermountain basins experience frequent temperature inversions.

Elevation, however, is not the only control on the climate of mountain regions. Proximity to moisture sources, as well as interception of moisture by other ranges, can exert strong influences on such factors as precipitation (Figure 23) and wind. The Rocky Mountains have a continental type climate, which is characterized by large ranges in temperature between summer and winter. The amount of continentality of a region is essentially dependent on its distance from the temperature moderating influence of the ocean and interception of ocean moisture by other mountain ranges. The prevailing air flow is from west to east in the temperate zone, which is where this paper is focused. Consequently, the eastern portion of the area is the most isolated from the Pacific Ocean and Pacific air masses, and thus experiences more extremes in temperature. During winter, in particular, Arctic air masses from Canada plunge southward over the Great Plains, at times bringing frigid weather to the eastern slope of the Rocky Mountains. The presence of the mountains often provides an effective barrier to the westward penetration of this air, keeping most of the Rocky Mountains and the Great Basin under the influence of milder Pacific air. In this way, the Rockies are a major climatic divide between the extreme continentality of the Midwest and milder climate of the Great Basin (Thornthwaite 1931; Trewartha 1943; Barry 1981).

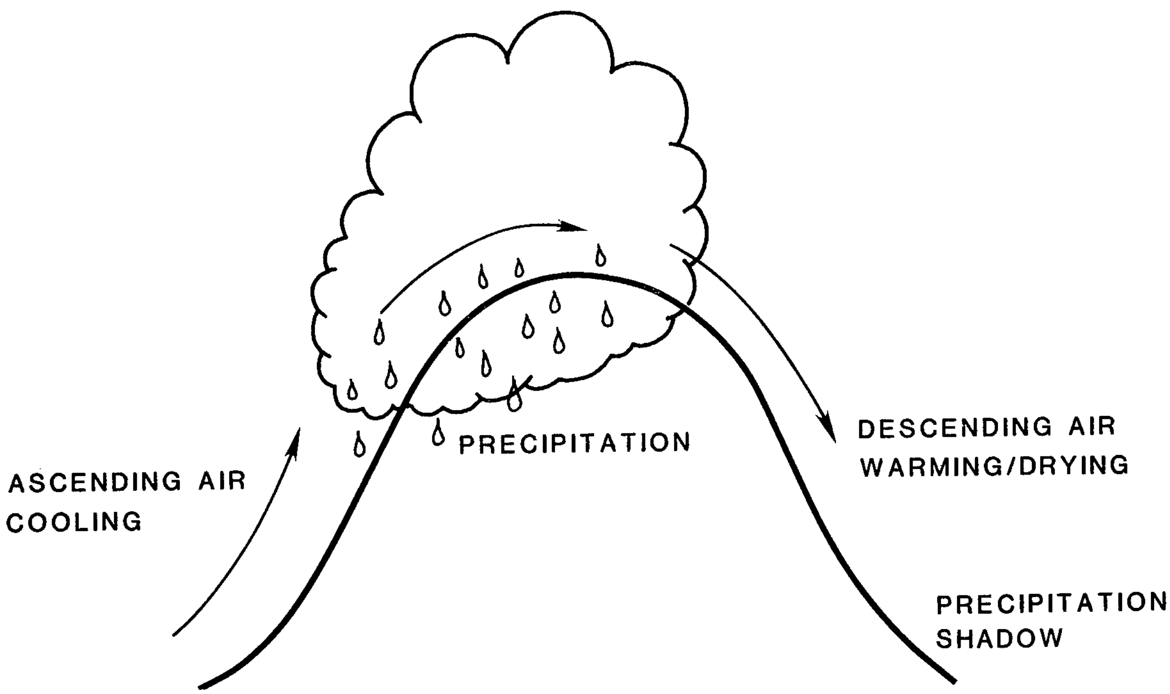


Figure 22. Typical patterns of cloud formation and precipitation in the Rocky Mountains. (By L. P. Rink.)

Figure 23. Mean annual total precipitation for the Rocky Mountain region in comparison to the United States. (From Baldwin 1973.)

Commonly, precipitation increases with elevation in the Rocky Mountains, although this general trend is modified very strongly by local conditions. For example, as air flows over mountains, it rises and cools, decreasing its ability to hold moisture. Once air reaches saturation, clouds form and precipitation results (Figure 22). This happens most often on west-facing slopes when moist Pacific air masses move eastward across North America. Figure 24 is an excellent example of a strong Pacific storm system that enveloped portions of Colorado in winter storms in December 1981. In this case, strong westerly winds in the upper atmosphere, heavy with Pacific moisture, followed a low pressure system centered in southeast Colorado. Strong uplift forced by the topography caused heavy snowfall over the mountains. Crested Butte, Colorado, received 53 cm (21 in) of snow over a short period of time. After crossing the Continental Divide, strong winds forced downslope created 160 kph (100 mph) gusts in Boulder. As air descends the eastern slope, the air warms and dries, placing the eastern slope in a precipitation shadow. Thus, during winter, when westerlies are strongest, western slopes of the Rocky Mountain ranges experience their wet season with heavy snows, while eastern slopes of ranges, especially those adjacent to the High Plains, are dry.

In spring, this west-wet/east-dry situation is frequently reversed as moist Gulf of Mexico air circulates counterclockwise north, then westward and upslope, where the air cools and deposits heavy wet snows on the eastern ranges. Figure 25 illustrates a typical upslope storm in Montana. A strong low pressure system centered in Colorado pumped moist air from the Gulf of Mexico in a counterclockwise direction northwestward over the plains into Montana, where higher topography lowered the temperature of the air mass and caused precipitation as wet, heavy snow. This storm dropped 15 cm (6 in) to 30 cm (12 in) of snow across the mountains. Table 9 compares monthly precipitation in two cases for stations located at the same latitude but on opposite sides of a mountain range. Data show that west slope stations experience wet months during winter, whereas east slope stations experience a wet season during the spring. The Colorado Front Range receives 40% of its total annual moisture from Gulf of Mexico storm systems (Marr 1967). Table 10 gives proportional distribution of precipitation by air mass.

Large intermountain basins, enclosed on most sides by mountains that create precipitation shadows for air coming from various directions, are the driest portions of the Rocky Mountains. For example, San Luis Valley, Colorado, receives less than 18 cm (7 in) of precipitation a year, in spite of its elevation of 2,500 m (8,200 ft) (see Figure 9) (Baldwin 1973). This is in marked contrast to west-facing slopes at equivalent elevations in the San Juan Mountains to the west, which receive more than 100 cm (40 in) a year. This shows that precipitation is not simply dependent upon elevation in the Rocky Mountains, but that exposure and sheltering by other ranges exert strong influences (see Figure 10). Similar slope-versus-basin contrasts occur throughout the whole of the Rockies from Montana to New Mexico.

SUNDAY, DECEMBER 27, 1981

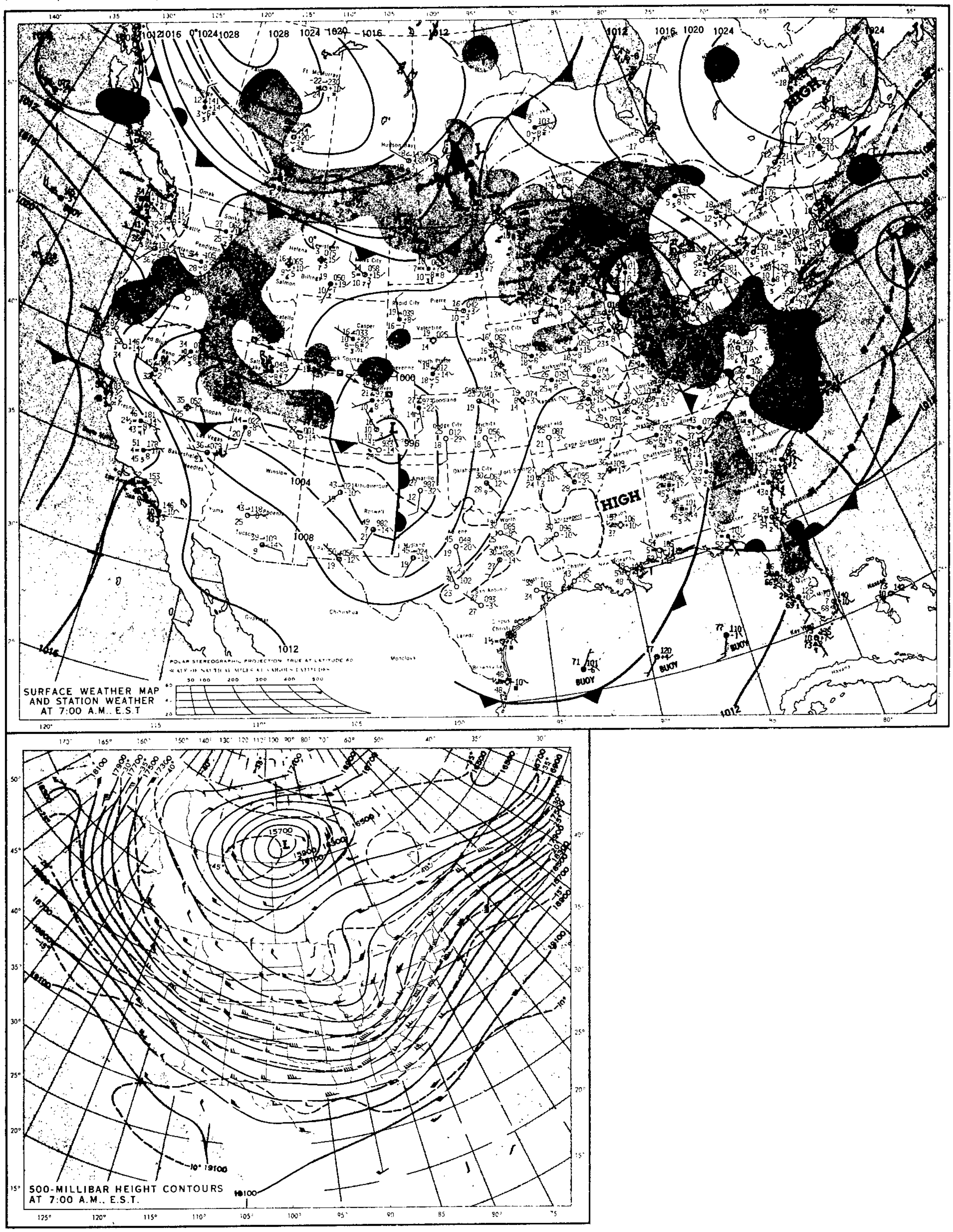


Figure 24. Weather maps from 27 December 1981. The 500-millibar height contours are approximately 5,490 m (18,000 ft) elevation. A Pacific air mass causing an upslope on the western slope in Colorado. (From U.S. Department of Commerce 1981.)

SUNDAY, MARCH 3, 1985

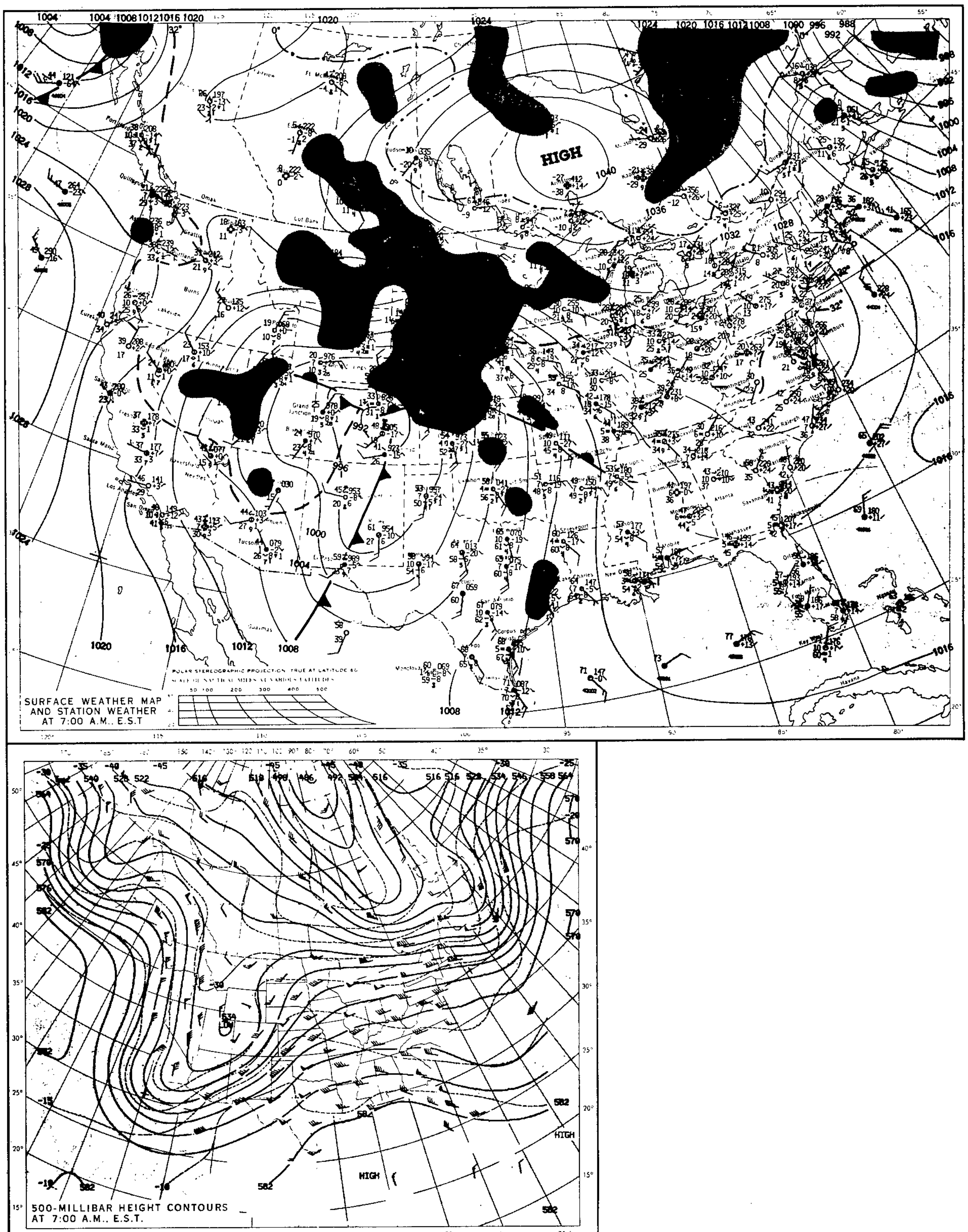


Figure 25. Weather maps from 3 March 1985. An eastern slope upslope storm in Montana. (From U.S. Department of Commerce 1985.)

Table 9. Comparison of monthly (seasonal) precipitation patterns at stations affected by different storm systems. (From Berry 1968; Cordell 1971.) Cases I and II compare two locations at approximately the same altitude but opposite sides of the Continental Divide. Northlake, in Case III, is a relatively isolated area, surrounded by mountains, which experiences late summer convective events.

Station	Mean monthly precipitation (cm)												Average annual total
	January	February	March	April	May	June	July	August	September	October	November	December	
<u>Case I</u>:													
Como Creek [E]	4.83	4.90	7.09	7.72	[9.55]*	8.36	8.15	6.17	5.61	4.72	5.44	4.52	77.06 (30.34")
Steamboat [W]	6.12	5.87	5.77	5.97	4.61	3.96	3.56	3.78	3.76	4.55	4.83	[6.22]	59.00 (23.23")
<u>Case II</u>:													
Babb [E]	2.03	2.31	2.69	3.96	6.55	[10.26]	4.14	4.42	5.03	3.20	2.69	2.36	49.64 (19.56")
West Glacier [W]	7.95	6.15	4.60	4.75	5.99	7.67	3.23	3.38	4.80	6.71	7.77	[8.28]	64.82 (25.52")
<u>Case III</u>:													
Northlake [E]	2.34	2.90	4.47	5.84	6.43	3.50	7.49	[7.57]	3.63	3.20	2.34	1.96	51.67 (20.36")

Case I:

<u>Como Creek</u> = the subalpine station of the University of Colorado Institute of Arctic and Alpine Research (INSTAAR), 12 miles west of Boulder, Colorado, on east side of Colorado Front Range at 3,050 m (10,000 ft elevation) 40.1 °N latitude.

<u>Steamboat</u> = Steamboat Springs, 200+ miles west-northwest of Boulder, Colorado, on west side of Park Range at 2,065 m (6,770 ft elevation) 40.5 °N latitude.

Case II:

<u>Babb</u> = at east base of Lewis Range, Montana, on plains at 1,310 m (4,300 ft) elevation, 49.9 °N latitude.

<u>West Glacier</u> = at west base of Lewis Range, Montana, on edge of Kalispell intermountain basin at 962 m (3,154 ft) elevation 48.5 °N latitude.

Case III:

<u>Northlake</u> = near southeast end of Sangre de Cristo Range near Culebra Peak, Los Animas County, Colorado, 60 miles west of Trinidad at 2,684 m (8,800 ft) elevation, 37.2 °N latitude.

*Brackets are around high precipitation times to provide emphasis.

Table 10. Distribution of annual precipitation by air mass type, Colorado Front Range. (From Marr 1967.)

Pacific air masses	15%
Canadian air masses	4%
Gulf of Mexico air masses	40%
Convectional storms	35%
Gulf of California air masses	6%

Another effect of mountains on precipitation is related to summertime air convection (Barry 1981). During summer, plains, basin, and mountain surfaces become strongly heated by solar flux; air above these surfaces becomes warmer than adjacent air above valley floors. This warm air evaporates water from water bodies and from vegetation on land surfaces. Since this warm air is less dense, and more humid, it rises and forms cumulus clouds as it cools with elevation. These clouds bring heavy showers to upper slopes (Figure 26), often several times each day. This rising air is replaced by air moving upslope (anabatic) from the surrounding lowlands (Figure 26b). Daytime winds generally reverse at night and flow downslope (katabatic), due to cold air drainage (Figure 26a). Northlake, Colorado, data show the effect of convective summer precipitation (Table 9).

The Big Thompson River, on the east slope of the Colorado Front Range, flooded on July 31, 1976. A strong, stationary high over Colorado and Canada collected moisture from lows located over both the Gulf of California and Gulf of Mexico coasts (Figure 27). Previous summer solar heating strengthened convection, added moisture aloft, and produced cumulus clouds that broke in a disastrous cloudburst, causing a 330-year flood event that cost 139 lives and $29 million damages (Henz and Cheetz 1976).

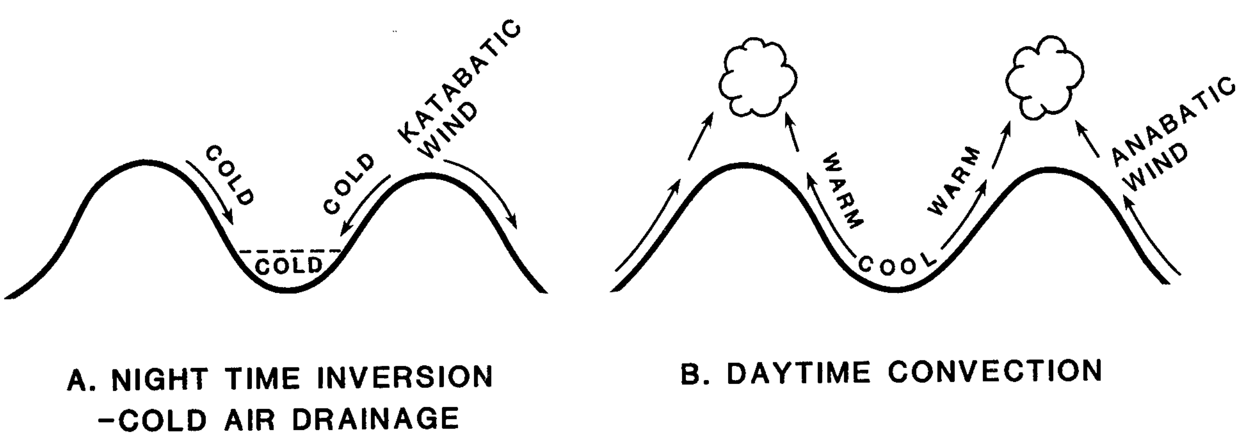


Figure 26. Inversion and convection weather patterns in the Rocky Mountains often results in pools of cold air in high mountain valleys.

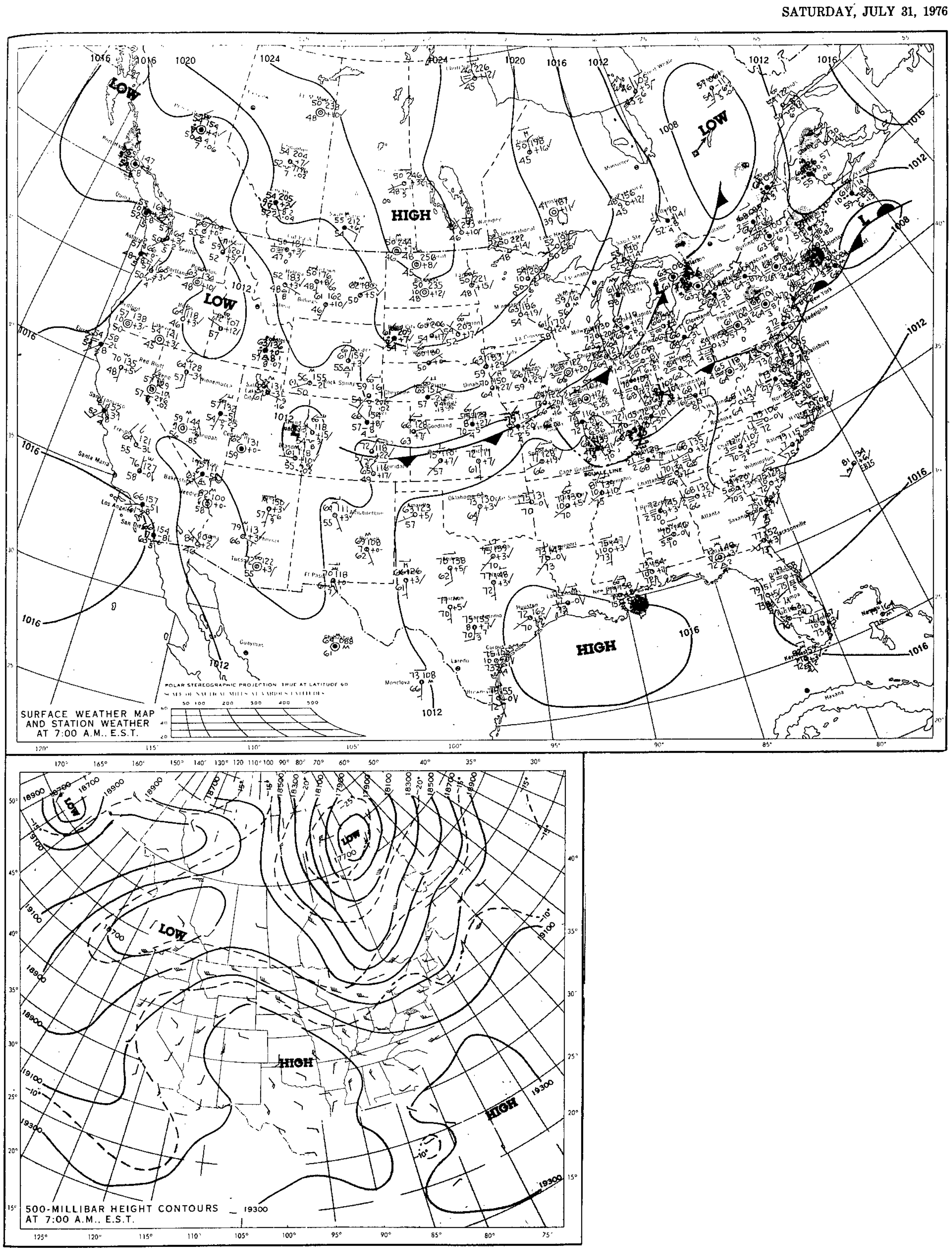


Figure 27. Weather maps from 31 July 1976--the day of the Big Thompson River flood, Colorado. (From U.S. Department of Commerce 1976.)

Increase in precipitation with elevation, along with a decrease in evaporation due to lower air temperature, allows for more available moisture in mountains. This can result in extensive forests in the mountain ranges as compared to grasslands on nearby plains and intermountain basins.

High windspeeds observed on exposed ridgetops cause high rates of evaporation, transpiration, and redistribution of snow, which can result in relatively dry local environments (Marr 1967). In contrast, adjacent depressions, cirques, and valleys can have higher humidity, lower evapotranspiration, and more snow accumulation.

In the Rocky Mountains, as in all mountains, exposure to solar radiation is another important influence on weather and local environment (Geiger 1959). South-facing slopes of the Rockies receive more solar radiation throughout the year than other slopes. As a consequence, these slopes experience higher temperatures, more rapid snowmelt, and higher evaporation than do north-facing slopes, especially in winter when solar rays approach perpendicular on some south-facing surfaces. Some places on north-facing slopes have no direct solar radiation in winter; consequently they retain snow all winter. This difference is commonly expressed in vegetation variations that are most noticeable at lower elevations (Marr 1967). For example, in east-west trending canyons of eastern slopes, moss and lichen flora on the damper, cooler north-facing slopes include the same species that are found along coasts of southern Alaska and Norway. A few hundred feet away on warmer, drier south-facing slopes, moss and lichen flora contain species found in high, cold deserts like the Great Basin and the Gobi Desert (Weber 1965). At lower elevations, there are differences in environment between east-facing and west-facing slopes caused by the prevalence of afternoon thunderstorms in eastern ranges, which reduce the afternoon intensity of solar flux. These examples emphasize the importance of local conditions, or microclimate, in determining the character of specific mountain environments (Geiger 1959).

2.4 HYDROLOGY OF THE ROCKY MOUNTAINS

Precipitation comes to watersheds of the Rocky Mountains, in several forms, on a seasonal basis. The most abundant form of precipitation is snow, followed by rain, hail, and, finally, dew or fog (Marr 1967).

Most snow falls from October through May (Owens 1980). At higher elevations, up to 80% of the annual precipitation is snow (Johnston and Brown 1979). The percentage decreases somewhat with elevation.

Direct snowfall measurements may not accurately represent real snow accumulation rates, primarily due to snow redistribution by wind (Marr 1967; Despain 1973; Johnston and Brown 1979). In alpine regions of the southern (Heifner 1974) and central (Leaf 1975b) Rocky Mountains, wind scouring of exposed terrain has been documented. Snow is blown from exposed sites and accumulates in depressions on lee slopes. Snow redistribution is greater in alpine regions due to greater wind fetch, direct impact of wind, greater wind velocities, and less influence of vegetation at alpine elevations (Marr 1967; Willard 1979).

Snowmelt in the central Rocky Mountains begins in late May and June (Despain 1973), with subalpine and alpine regions experiencing a 3- to 4-week delay relative to montane slopes (Johnston and Brown 1979). Snowmelt is about 2 to 3 weeks earlier in the southern Rocky Mountains (Marr 1967).

Exposure to sunlight is an important factor influencing rates of snowmelt. Snowmelt is more rapid in patchcut versus uncut forests (Leaf 1975b). There is little difference between east versus west exposures; however, snowmelt on northern exposures lags behind southern exposures. Excessive shading in afternoons, which occurs in steep-walled cirques and on north-facing slopes permits snowbanks to persist late into summer (even from year to year), creating a more constant water source for wetlands. The time lag between northern and southern exposures decreases with elevation (Leaf 1975b).

Rain occurs as summer thunderstorms or from late spring/summer upslope Gulf of Mexico storms. The greatest frequency of thunderstorms is from May through July (Owens 1980). Rainfall rates generally increase with elevation (Despain 1973) and can be extremely variable throughout the Rocky Mountains. Autumns are often short and dry, but may be interrupted by snowstorms from the Gulf of Mexico. Most water from snowmelt runs off before the growing season is well underway in mountain wetlands, making summer precipitation or late season snowmelt extremely important for the maintenance of many types of wetlands.

Subsurface hydrology or groundwater varies greatly throughout the Rocky Mountains, dependent on geology, watershed topography, soil characteristics, and season. Depth to water table reflects the capacity for vertical drainage of a given area. Less drainage to groundwater results in a greater proportion of surface runoff.

In subalpine regions where soils are thin, collected surface water is rare and the water table essentially nonexistent (Wilson 1969). Seepage slopes are common (Wilson 1969) and can result in solifluction lobe formation at higher elevations. Glacial valleys characterized by glacial and alluvial accumulation often have a shallow depth to water table. High groundwater tables have also been observed in intermountain basins where sediments are porous, gradients low, and internal drainage frequent.

2.5 ROCKY MOUNTAIN SOILS

As might be expected, the diversity of Rocky Mountain environments, elevations, rock types, and erosional histories makes for a complex mosaic of discontinuous and heterogeneous soil types (Retzer 1962; Price 1981). Within each site, biotic and abiotic factors interact to continue producing the soil profile observed at present. Primary factors influencing soil development include climate, vegetation type, primary productivity, length of growing season, topography, parent material, groundwater, erosional history, and time.

In the Lower Montane Life Zone and intermountain basins of the Rocky Mountains, the precipitation-evaporation (P-E) balance is typically less than 1, allowing for development of pedocal soils. In the Upper Montane and Subalpine Life Zones, where snowpack persists, at least in places, the P-E balance exceeds 1 and pedalfers are formed (Marr 1967). Through a system of soil classification developed in the United States (known as the "7th approximation"), Rocky Mountain soils can be further categorized into five major groups, based entirely on soil morphology. Entisols describe undeveloped soils, for example, soils found on bare rock surfaces or those formed from fragmented bedrock or unconsolidated material such as talus, recent glacial moraine and sandbars. The mollisols and inceptisols may occur in subalpine meadows displaying a relatively deep, tight organic root zone. Histosols, or bog/peat soils, form where drainage and oxidation is poor and peat accumulates, as in some wetland areas. Spodosols, a moderately deep, well-drained and developed soil type, occur in the subalpine where organic input and accumulation are relatively high (Price 1981).

CHAPTER 3

COMMUNITY STRUCTURE AND CLASSIFICATION OF ROCKY MOUNTAIN WETLAND ECOSYSTEMS[1]

3.1 INTRODUCTION

Wetlands in the Rocky Mountain Province do not occur as regional climaxes due to the continental or modified continental climate of the region. In North America, climax wetlands in mountains occur throughout the Arctic and sub-Arctic, where permafrost helps keep soils saturated, and also in cool to cold extreme maritime regions, such as Alaska's Aleutian Islands. In the Rocky Mountains, runoff is rapid and precipitation, humidity, and cloud cover are generally low. Waterlogged soils and wetland species can survive only in special topographic sites where abundant water occurs seasonally or permanently. These ecosystems are topoedaphic climaxes, according to Marr (1967).

Rocky Mountain wetlands can have either mineral soils or organic soils. Wetlands on organic soils are usually termed moors or peatlands (Heinselman 1963). Large areas with organic soils are almost totally restricted to valley bottoms and intermountain basins, due to absence of hydric conditions in the uplands. Because regional precipitation and humidity are low, peat-forming mosses and sedges grow slowly. Lack of permafrost throughout nearly all Rocky Mountain montane and subalpine wetlands permits more drainage and leads to warmer soil temperatures than occur in sub-Arctic wetlands. Where aeration is sufficient for microbial activity, decomposition of peat may be rapid, reducing accumulation. Wetlands on mineral soils usually occur where alluvium is being deposited on a floodplain more rapidly than peat is accumulating, or where oxidation of organic matter is relatively rapid.

3.2 WETLAND CLASSIFICATIONS

In the United States, since 1956, wetlands have been classified using the system presented in Circular 39 (Shaw and Fredine 1956). The shortcomings of this system have been discussed by Leitch (1966) and Stewart and Kantrud (1971), among others. The shortcomings include: (1) failure to adequately define wetland types, resulting in inconsistencies in application; (2) oversimplification such that some critical ecological differences between certain types have been ignored; and (3) primary emphasis on wetland vegetation used by waterfowl, which omits many wetland types.

[1]Authored by D. J. Cooper.

Several other classifications have been devised since 1956, some of which deal only with wetlands, for example, Golet and Larson (1974) for the northeastern U.S., Millar (1976) and Stewart and Kantrud (1971) for portions of the Great Plains, Goodwin and Niering (1975) for inland areas of the U.S., and Zoltai et al. (1975) for Canada. Other vegetation classification schemes deal with more than just wetlands, for example, Brown et al. (1979) and Driscoll et al. (1984).

A recent classification of U.S. wetlands by Cowardin et al. (1979) has been created for use by the U.S. Fish and Wildlife Service. The Cowardin classification describes five large systems, three of which (lacustrine, palustrine, and riverine) occur in the Rocky Mountain region. The lacustrine and riverine systems are divided into subsystems: littoral and limnetic for the lacustrine system, and upper and lower perennial and intermittent for the riverine system. Class is the third level of the Cowardin system; it is based on a combination of substrate types and life-forms of dominant species. Below the class level is dominance type, characterized by the dominant plant and/or animal species. The Cowardin classification also includes modifiers to describe specific aspects of water regime, water chemistry (salinity and pH), soil, and special situations, such as beaver ponds or agriculture. These authors state that their "initial attempt to use familiar terms, such as marsh, swamp, bog, and meadow at the class level were unsuccessful primarily because of wide discrepancy in the use of defining these terms in various regions of the U.S." Instead of defining these terms they avoided the conflict and confusion by inventing new terms.

The classification presented here (Table 11) is a modified version of the Cowardin system. Table 12 shows how a variety of wetland classification systems compare with the system used in this report and with each other. Wetlands have been investigated in Europe, Scandinavia, and the U.S.S.R. for much longer than in the U.S., and terms such as fen and bog have been clearly defined and used throughout these parts of the world. Most researchers in Canada, Alaska, and some other parts of the U.S., e.g., Heinselman (1963), utilize these international terms as the basis for their research and classifications with great facility and success. We use the international system of nomenclature, define the terms used, and expect anyone using this volume to learn and use these terms in their scientific sense, _not_ a colloquial sense. Terms like fen and bog are placed at the highest classification level in the present system, the ecosystem type. Community type, which is based on floristics, is placed at the second level of classification.

In the Rocky Mountains, ecosystems associated with moving and nonmoving water have different ecological processes and form distinctly different communities. Streams and rivers have relatively high oxygen and may have high nutrient contents, and their energy signatures (_sensu_ Odum et al. 1974, 1977) occur nowhere else. Using the Cowardin system, it is impossible to differentiate, except at the dominance-type level, between a shrub wetland or carr found below a late-lying snowbed in the subalpine zone and dominated by _Salix planifolia_, and a streamside shrub wetland dominated by _Alnus tenuifolia_ and _Betula occidentalis_, although their only real ecological similarity is dominance by shrubs. A distinct zone influenced by the high oxygen and nutrient content and the energy signature associated with moving water does

Table 11. Classification of Rocky Mountain wetland communities in this paper.

Categories of Rocky Mountain wetlands	Subcategories	Substrate	Water type	Ecosystem types
Permanent shallow standing water	Floating	Water	Depends on elevation, bedrock type, and age of water body.	Not applicable
	Rooted submerged	Mineral or organic		Not applicable
	Rooted floating-leaved	Mineral or organic		Not applicable
	Rooted emergent	Mineral or organic		Not applicable
	Unvegetated wetlands	Mineral		Not applicable
Communities with seasonal or permanent high tables, but without permanent standing waters	Herb wetlands	Organic	Minerotrophic Ombrotrophic	Fen Bog
		Mineral	Fresh Saline	Marsh-meadow Saline marsh-meadow
	Shrub wetlands	Organic	Minerotrphic Ombrotrophic	Carr Shrub bog
		Mineral	Fresh Saline	Shrub wetland Saline shrub wetland
	Forested wetlands	Organic or mineral	Fresh Fresh	Deciduous angiosperm forest
	Unvegetated wetlands	Mineral	Fresh and salt	None
Communities adjacent to running waters	Moss wetlands	Mineral or organic	Fresh	Moss wetlands
	Herbaceous wetlands	Mineral or organic	Fresh	Herbaceous wetlands
	Shrub wetlands	Mineral or organic	Fresh	Shrub wetlands
	Forested wetlands	Mineral or organic	Fresh	Coniferous forest Deciduous angiosperm forest
	Unvegetated wetlands	Mineral	Fresh and salt	None

Table 12. Comparison of wetland and land classification systems by various authors.

Cooper[a] (1986)	Cowardin et al. (1979)	Nat'l. Wetlands Inventory Legend (1979)	Brown et al. (1979)	Zoltai et al. (1975)	Goodwin & Niering (1975)	Shaw & Fredine (1956)	Driscoll et al. (1984)
SHALLOW OPEN WATER COMMUNITIES	LACUSTRINE	---	---	Shallow open water	---	---	---
Floating	Aquatic bed or unconsolidated bottom; permanently flooded; fresh mixosaline, saline, or eusaline	L2AB4	---	---	Deep freshwater and open saline marshes	Type 5-inland open fresh water marshes,	Free-floating freshwater, herbaceous vegetation
Rooted submerged	Same	L2AB3	Rocky Mountain alpine, subalpine, and montane submergents	---	Deep freshwater and saline marshes	---	Rooted hydromorphic freshwater vegetation
Rooted floating	Same	L2AB3	Rocky Mountain alpine, subalpine, and montane submergents	---	Deep freshwater and saline marshes	---	Rooted hydromorphic freshwater vegetation
Rooted emergent	Same	L2EM1F	Rocky Mountain alpine, subalpine, and montane marshland and lake strand	Marsh	Shallow fresh and saline marshes	Type 11-inland open freshwater	Rooted hydromorphic freshwater vegetation

Table 12. (Continued)

Cooper[a] (1986)	Cowardin et al. (1979)	Nat'l. Wetlands Inventory Legend (1979)	Brown et al. (1979)	Zoltai et al. (1975)	Goodwin & Niering (1975)	Shaw & Fredine (1956)	Driscoll et al. (1984)
HIGH WATER TABLE COMMUNITIES	PALUSTRINE	---	---	---	---	---	---
Fen	Emergent, saturated, fresh or mixosaline water, organic soil	PEM1Bt/1g	Rocky Mountain alpine, subalpine, and montane marshland	Fen	Fresh meadows	Type 2-inland fresh meadows	---
Bog	Moss/lichen, fresh (acidic) water, organic soil	PEM1Bag	Rocky Mountain alpine and subalpine marshland	Bog	Bog	Type 8-bogs	---
Marsh, fresh water	Emergent, saturated, mixosaline water, soil	PEM1C0tn	---	Marsh	Seasonally flooded basins and flats	Type 3-4 inland shallow and deep fresh marshes	---
Marsh, saline water	Emergent, saturated, hypersaline water, mineral soil	PEM1C7/8/91n	Rocky Mountain alpine, subalpine, and montane marshland	Marsh	Saline marshes	Type 9,10 inland saline flats and marshes	---
Carr	Scrub/shrub, saturated, fresh or mixosaline water, organic soil	PSS1B9/01g	Rocky Mountain alpine, subalpine, and montane swamp and riparian scrub	Swamp	Shrub	Type 6-shrub swamp	Deciduous, peat shrubland

Table 12. (Continued)

Cooper[a] (1986)	Cowardin et al. (1979)	Nat'l. Wetlands Inventory Legend (1979)	Brown et al. (1979)	Zoltai et al. (1975)	Goodwin & Niering (1975)	Shaw & Fredine (1956)	Driscoll et al. (1984)
Shrub bog	Scrub/shrub, saturated, fresh (acidic) water, organic soil	PSS1Bag	Rocky Mountain alpine, subalpine, and montane swamp and riparian scrub	Bog	Bog	Type 8-bogs	---
Shrub wetland, mineral soil, fresh water	Scrub/shrub, seasonally flooded, fresh water, mineral soil	PSS1COn	Rocky Mountain alpine, subalpine, and montane swamp and riparian scrub	Swamp	Shrub swamps	Type 6-shrub swamps	Subalpine and alluvial shrubland
Shrub wetland, mineral soil, saline water	Scrub/shrub, seasonally flooded, hypersaline water, mineral soil	PSS1C7/8/9n	Rocky Mountain alpine, subalpine, and montane swamp and riparian scrub	Swamp	Saline shrub swamps	Type 9,10-inland saline flats and marshes	Deciduous shrubland
Coniferous forest	Forested, fresh water	PFO4ABOn	Rocky Mountain riparian forest	Swamp	Wooded swamps	Type 7-wooded swamps	Needle-leaved evergreen forest
Deciduous angiosperm forest	Forested, fresh water	PFO1A/BOn	Rocky Mountain riparian forest	Swamps	Wooded swamps	Type 7-wooded swamp	Montane cold-deciduous

Table 12. (Concluded)

Cooper[a] (1986)	Cowardin et al. (1979)	Nat'l. Wetlands Inventory Legend (1979)	Brown et al. (1979)	Zoltai et al. (1975)	Goodwin & Niering (1975)	Shaw & Fredine (1956)	Driscoll et al. (1984)
COMMUNITIES ADJACENT TO MOVING WATER	RIVERINE OR PALUSTRINE	---	---	---	---	---	---
Moss	Riverine, upper perennial, aquatic bed	R2/3/4ML1A-HO	Rocky Mountain alpine, subalpine, and montane stream strand				
Herbaceous	Palustrine, emergent, saturated, and/or palustrine, streambed	PEMBOg/n or PSB1-7AOn	Rocky Mountain alpine, subalpine, and montane stream strand	---	Riparian meadow	Type 1- seasonally flooded basins or flats	Forb-dominated herbaceous vegetation also grassland shrubland
Shrub wetland	Palustrine, scrub/shrub, fresh water, mineral soil	PSSBOg/n	Rocky Mountain alpine, subalpine, and montane riparian scrub	Swamp	Riparian shrub swamps	Type 6- shrub swamp	Subalpine and alluvial deciduous
Coniferous forest	Palustrine, forested, fresh water	PFO1BOg/n	Rocky Mountain riparian forest	Swamp	Riparian wooded swamps	Type 7- wooded swamp	Needle-leaved evergreen forest
Deciduous angiosperm forest	Palustrine, forested, fresh water	PFO1BOg/n	Rocky Mountain riparian forest	Swamp	Riparian wooded swamps	Type 7- wooded swamp	Montane cold-deciduous forest

[a]This publication.

not occur along all streams in the Rocky Mountains, but in many areas it is the only wetland vegetation occurring along upper and lower perennial streams. We think that important ecological features such as organic vs. inorganic soils, minerotrophic vs. ombrotrophic water source, and the type of water regime should be primary determinants for the classification. The classification system presented here is based on these primary ecological differences (Table 11).

In the Rocky Mountains, the Riverine System, as described by Cowardin et al. (1979), usually consists of animal- and algae-dominated communities on submerged rocks. The aquatic bed class of Cowardin generally does not occur in the Rockies, except where mosses cover rocks, but these are not always true aquatic mosses. We do not treat algae- or animal-dominated communities.

This classification of wetlands was developed specifically for the Rocky Mountains. It is based on a combination of ecology, floristics, and life form. Two groups of factors are of primary importance in determining the patterns of species and communities: (1) duration, depth, velocity of water, and frequency of flooding; and (2) variety and concentration of mineral nutrients in the water. These factors interact to control soil aeration, availability of minerals (including salts), accumulation or oxidation rates of peat, and rates of floodplain erosion and sediment deposition.

Three major groups of wetland communities occur in the Rocky Mountains: (1) communities with permanent standing water, (2) communities adjacent to moving water courses, and (3) all other communities with seasonally or permanently high water table. Within the permanently shallow water and adjacent to running water categories, the classification is structured around life form. Parameters used to classify other communities are organic vs. mineral soil, soil salinity, and minerotrophic vs. ombotrophic water source, together with life form of the dominant plant species.

3.3 WETLAND ECOSYSTEMS

Communities Located in Permanent Shallow Standing Water

Permanent shallow standing water is defined here as water less than 2 to 4 m (6.6 to 13.1 ft) in depth that can support either floating or anchored plants. Both Cowardin et al. (1979) and Zoltai et al. (1975) use 2 m (6.6 ft) as the lower limit of shallow open water communities, but rooted vegetation in deeper water is reported from the U.S. (Davis and Brinson 1980). The water may be in a lake or pond, which may or may not be located along a stream course. Standing water for much or most of the growing season is characteristic.

Early in a hydrosere, the dominant environmental factor controlling the distribution of organisms and communities is the depth of water in relation to light availability on the pond bottom (Daubenmire 1968). Later in the sere, however, mineral nutrition, aeration, and temperature of the rooting medium are more influential. The substrate type is also important in the sere,

whether it is silt, sand, or cobble, because different species grow better on different substrates. These physical conditions and the types of colonizing species may determine the rate and pattern of succession.

The question of whether shallow-water plants with different life forms overlap or form distinct zones in lakes has received considerable attention. In high elevation Rocky Mountain lakes, many zones may be missing, e.g., any or all of the floating, rooted floating-leaved, or rooted submerged zones. Large emergent species such as *Typha* spp. and *Scirpus* spp. are also lacking in many areas, especially in the Subalpine Zone.

Floating communities. The center of stagnant ponds that are too deep or turbid for rooted plants may be populated by communities of floating plants and animals. Dominant vascular plants may include species such as *Lemna minor* and *L. trisulcata*. The depth of water is of no consequence to floating plants; they occur where the wind pushes them. Community composition and structure may change from hour to hour, yet the environment, which is mainly the top few centimeters of water, is homogenous. These organisms are especially abundant under eutrophic conditions where nutritive material is abundant (Weber 1976). Floating plants were not reported from Redrock Lake in Colorado's Front Range at 3,080 m (10,105 ft) elevation (Ramaley and Robbins 1909). However, an *L. minor* - *L. trisculcata* community occurs in ponds in the Jackson Hole, Wyoming, area (Reed 1952).

Because the biomass of floating organisms is generally not great, they do not have an important influence on the accumulation of organic matter on pond bottoms. Perhaps their major impact on successional processes is to limit or eliminate light penetration, restricting the development of more advanced communities on the pond bottom (Daubenmire 1968).

Rooted submerged communities. Where light penetrates to the pond bottom and where the water depth is less than several meters, the first macrophytes to invade are usually submerged rooted species. They compose the innermost zone of vascular plants in pond margin vegetation (Figures 28, 29) and, because they are totally submerged (often at considerable depth), they are poorly known in the Rocky Mountains.

Light intensity usually limits the depth at which submerged communities may grow. The compensation point of light, where photosynthesis and respiration are in balance, should limit the lower depth distribution of a species (Davis and Brinson 1980); however, this may be secondary to the type of substratum (Pearsall 1920, 1929). For example, in ponds with high organic substrates the ooze severely restricts establishment of aquatic macrophytes (Davis and Brinson 1980). *Isoetes* spp. and *Nitella* spp. are characteristic on poor and coarse silts, whereas *Potamogeton* spp. and *Najas flexilis* are characteristic on finer and richer soils (Pearsall 1929).

Submerged species act as sediment traps because of their effectiveness in reducing flow velocities. Silt may accumulate on the leaves of some broad-leaved submerged species, such as *Myriophyllum exalbescens*, reducing light and gas exchange to the leaves, and increasing weight on them, thus controlling its distribution (Schiemer and Prosser 1976). Species with narrow leaves, such as *Potamogeton filiformis* or *P. vaginatus*, are less affected by siltation.

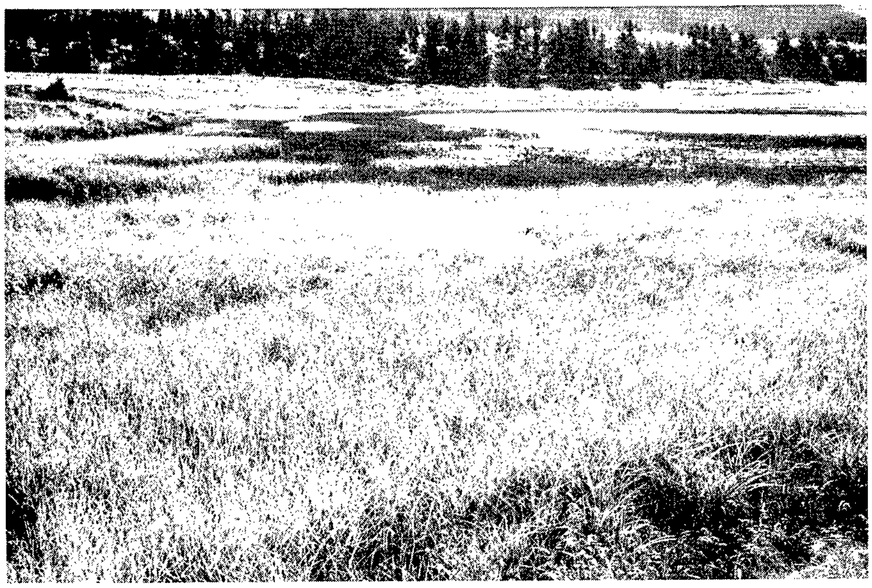


Figure 28. Distinct zonation of vegetation can be seen around pond on Kenosha Pass, Colorado Front Range. (Photo by D. J. Cooper.)

Figure 29. Zonation of vegetation around pond on Kenosha Pass, Colorado Front Range. The lake is filled with a rooted submergent community. A rooted emergent community dominated by Eleocharis macrostacha and a fen dominated by Carex utriculata are in the foreground. (Photo by D. J. Cooper.)

Submerged species may escape freezing temperatures by colonizing below the zone of ice formation and may remain intact, although with little growth, through the winter season.

Waterfowl feed largely on submerged species and can remove up to 40% of the peak standing crop of foliage (Anderson and Low 1976).

In a comparison of Rocky Mountain and Illinois pond communities, Fuller (1930) found that similar community types in Illinois ponds may have twice the number of species and biomass found in Colorado ponds. Fuller reported that the main submerged communities in Colorado lakes were the _Myriophyllum exalbescens_ - _Ranunculus trichohpyllus_ community, and communities dominated by _Sparganium angustifolium_, _Potamogeton longchitis_, and _P. foliosus_. _Isoetes bolanderi_ occurs in submerged communities in Dream Lake 2,904 m (9,520 ft) and several similar lakes in Rocky Mountain National Park, Colorado (Willard 1985). _Potamogeton filiformis_ dominates the lake area around Lake John, in Colorado's North Park (Johnson 1941). _Sagittaria arifolia_, _Potamogeton filiformis_, and _Persicaria coccinea_ are the dominant species in ponds around Aldrich Lake, Colorado (Johnson 1941). _Ranunculus reptans_ and _Callitriche_ sp. dominate the lake zone around Grand Lake, Colorado (Johnson 1941). _Callitriche palustris_ and _Ranunculus trichophyllus_ dominate the vegetation in oxbow ponds in Colorado's Boulder Park (Robbins 1918). _Ruppia maritima_ may be the only submerged vascular plant species to occur in lakes with saline water (Bolen 1964).

Most rooted, submerged macrophyte species appear to be limited to the Upper Montane and Lower Montane zones, and the intermountain basins where warmer water occurs. Many submerged vascular plant species, such as _Myriophyllum exalbescens_, _Hippuris vulgaris_, _Ranunculus trichophyllus_, are cosmopolitan, circumpolar, boreal, and temperate zone species (Hulten 1968), and similar communities will be found throughout the Northern Hemisphere. Although communities dominated by _Hippuris vulgaris_, _Utricularia vulgaris_, and numerous other characteristic wetland taxa are not reported in the literature, they are known to occur in the field.

Rooted floating-leaved communities. Where pond water is less than 2 to 3 m (6.6 - 9.8 ft) in depth, and where little wave action occurs, plants that are rooted in the pond bottom and whose leaves float on the pond surface can dominate. Important species include _Nuphar luteum_ ssp. _polysepalum_, _N. variegatum_, _Nymphaea tetragona_, _Sparganium angustifolium_, and some species of _Potamogeton_. Leaves may be dense enough to cover nearly the entire pond surface, but more typically they are scattered (Figure 30).

Exposure of the tops of leaves to sun and wind has led to development of a cuticle and lignification of xylem in species such as _Nuphar luteum_ ssp. _polysepalum_ (Daubenmire 1974). Dead tissues of these plants are slower to decay and thus add more substance to pond bottom soils.

Figure 30. Rooted floating-leaved Nuphar luteum ssp. polysepalum dominates a zone just offshore in Cub Lake, Rocky Mountain National Park, Colorado. This community is common in shallow lakes with a sluggish drainage in the high Montane and low Subalpine zones. (Photo by B. E. Willard.)

Communities dominated by Sparganium angustifolium occur throughout boreal and mountain regions of North America. In Colorado's Sawatch Range at 2,745 - 3,050 m (9,000 - 10,000 ft) elevation, S. angustifolium dominates ponds with greater than 20 cm (7.9 in) of standing water in midsummer (Cooper 1986); and it dominates the second stage in glacial lake succession in Colorado's Boulder Park (Robbins 1918). Communities dominated by Nuphar luteum ssp. polysepalum are most abundant in low Subalpine and high Montane ponds (Weber 1976), but this species is not consistently present in ponds with appropriate environments. It forms communities with Ranunculus natans, Glyceria borealis, and Potamogeton epihydrus in lakes near Jackson Hole, Wyoming (Reed 1952). It is also a dominant feature of the midsummer vegetation on Colorado's Redrock Lake (Ramaley and Robbins 1909).

Rooted emergent communities. Vascular plants that are rooted in ponds or lakes and whose stems protrude above the water surface are included in this category (Figure 28). Typically, rooted emergent communities include species of Carex, Eleocharis, Juncus, Glyceria, Phragmites, Sagittaria, Scirpus, Sparganium, and Typha and are frequently termed "reed swamps" (Moss 1955). Species in this group are "amphibious," as opposed to the "aquatics" in the previous three community types. All species that fall into this category can be pioneers in shallow water, on mud, or follow submerged or floating rooted hydrophytes in hydroseres. As pond water becomes more shallow, these plants are able to encroach on the floating leaved plants by sending shoots up into the air between their blades (Daubenmire 1974). In many hydroseres in the high mountains this is the first zone of wetland vegetation and forms a ring around many lakes.

Rooted emergent species vary in size from 10 - 20 cm (25.4 - 50.8 in) tall in Eleocharis acicularis and Triglochin palustre, to Carex aquatilis and C. utriculata, which are up to 50 cm (1.6 ft) tall, to Scirpus lacustris and Typha latifolia, which can be 1 to 3 m (3.3 - 9.8 ft) tall. Typically, one or a few species dominates a site, and the community is densely vegetated.

In Boulder Park, Colorado (Robbins 1918), Eleocharis acicularis invades and becomes dominant on bare mud along with Ranunculus reptans, whereas Carex aquatilis invades communities with some organic matter. In different areas, however, other species can invade bare mud, e.g., Carex utriculata, Juncus castaneus, or J. mertensianus. A number of species of Scirpus dominate emergent communities in the Rocky Mountains. Scirpus lacustris ssp. validus forms a bulrush zone at Lake John in North Park, Colorado (Johnson 1941). Scirpus paludosus occurs in more saline water in Utah (Flowers 1934; Nelson 1955; Bolen 1964) and elsewhere in the West (Figure 31).

Communities dominated by Menyanthes trifoliata occur in ponds along the Green Mountain Trail in Rocky Mountain National Park (Willard 1985). Petasites sagittata may entirely fill ponds in Boulder Park (Robbins 1918) and near Allenspark, in the Colorado Front Range, along Colorado Highway 7 (Figure 32).

Typha latifolia and T. angustifolia are probably the most abundant and widespread emergents found in the West. They occur in the mountain parks and intermountain basins and in the Foothills and Montane Zones in the mountains. They are abundant along roads, ditches, streams, and ponds. Typha has increased in Colorado's Monte Vista Wildlife Refuge where irrigation has occurred. A large-scale invasion of Typha may be precipitated by a temporary draw-down of the water in ponds during the growing season, which allows establishment of numerous seedlings on exposed mud flats (Nelson and Dietz 1966). Primary productivity in Typha communities may be as high as 1,400 g/m^2 (Bray 1960).

Typha is important nesting habitat for red-wing and yellow-headed blackbirds and marsh-wrens (Matsumura and Harrington 1955), and is the most important nesting cover for mallards in the San Luis Valley (Ryder 1951). Nesting success for waterfowl in Colorado's San Luis Valley was 83.4% in Typha, 61.7% in Scirpus, 60.7% in grasslands, and 36.7% in brushlands (Ryder 1951). Waterfowl nest density/41 ha (100 ac) in the San Luis Valley was 427.3 in Typha, 295.0 in Scirpus, 8.7 in grass, and 1.0 in hayland. The number of successful nests of American coot in Colorado ranged from 1.0 to 35.1 in Typha and Scirpus wetlands (Gorenzel 1979). Coots did not use Scirpus americanus, Carex, Eleocharis, Distichlis stricta, or Sparganium for nesting.

Flooded greasewood (Sarcobatus vermiculatus) stands in Colorado's Monte Vista National Wildlife Refuge may retain shallow water and have communities dominated by Juncus balticus. Ninety-eight percent of the mallard nests in this area are associated with Juncus and Sacrobatus (Anderson 1967; Enright 1971; Robinson 1971), and pintails, shovelers, teal, and gadwall also occur. The areas around the dead greasewood provided the most successful nesting habitat; Juncus 20 to 40 cm (7.9 - 15.8 in) in height was preferred, especially where it was dense enough to lodge (Enright 1971). Western grebes nested over water that had a minimum depth of 25 to 30 cm (10 - 11.8 in) on Manitoba's Delta Marsh. The nests were in wave-sheltered areas with a moderate

Figure 31. Scirpus paludosus dominates the rooted emergent zone around this saline pond in Colorado's San Luis Valley, at 2,623 m (8,600 ft) elevation. (Photo by D. J. Cooper.)

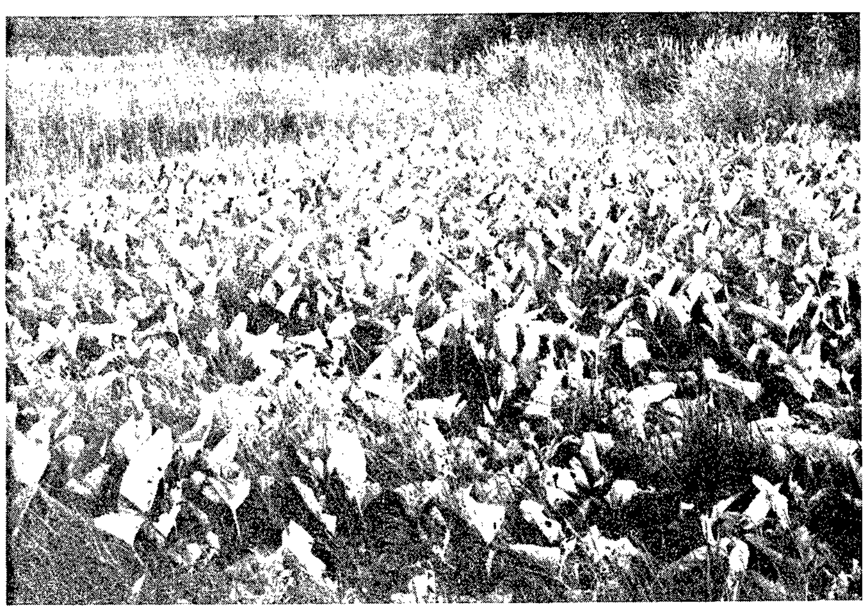


Figure 32. Petasites sagittata, a broad-leaved rooted emergent species, dominates this shallow pond near Allenspark, Colorado, at 2,593 m (8,500 ft) elevation. This is a rare community type. (Photo by D. J. Cooper.)

density of Scirpus. Western grebes avoided nesting in Phragmites australis. Phragmites is not common in the Rocky Mountains, but can be common elsewhere in the West.

The wood frog (Rana sylvatica) is a widespread boreal amphibian that occurs in northern Colorado, Wyoming's Bighorn Mountains, and northern Montana, where it most likely is a Pleistocene relict (Haynes and Aird 1981). It occurs around montane ponds in emergent vegetation dominated by Carex utriculata, C. aquatilis, Eleocharis palustris, Sparganium angustifolium, and several species of submerged vascular plants. Most egg masses were found in emergent vegetation dominated by Carex utriculata and Calamagrostis canadensis. Other amphibians occurring in this habitat include chorus frogs (Pseudacris triseriata), leopard frogs (Rana pipiens), boreal toad (Bufo borealis), and tiger salamander (Ambystoma tigrinum).

Unvegetated wetlands. Many mountain lakes and beaver ponds do not support vegetation. This is most likely because of the erosive action of waves or rapid siltation rates.

Communities with Seasonal or Permanent High Water Tables, but Without Permanent Standing Water

Herbaceous wetlands. Where standing water is present only early in the growing season or during wet weather periods, graminoid and herbaceous vascular plant species, or mosses, may form dense vegetation mats. On the edges of ponds, species of Carex and Sphagnum may form floating mats that can push out onto the water surface. Whether the vegetation mat is the floating kind or rooted in the pond bottom, it is very constructive in succession through the active formation of peat, and usually becomes the major contributor to sedimentation (Daubenmire 1968). A floating mat has an advantage over rooted emergent plants because it can maintain its position relative to the water surface as the water level changes through the seasons.

Herbaceous wetlands may override communities of emergent or submerged rooted plants. Vegetation on higher soils well back from the pond edge also continues to build up, becoming firmer and thicker with age. The higher soils are more well-drained and better aerated, which allows species that cannot tolerate continuously saturated soils to invade. The two most important environmental gradients affecting vegetation, floristics, and productivity of peatlands are the moisture-aeration and pH-nutrient regimes (Jeglum 1971). A major difference in wetlands is whether they have an organic or a mineral soil.

Definitions of mineral and organic soils follow from Cowardin et al. (1979) and the Soil Survey Staff (1975).

Mineral soil material is defined as follows:

(1) never saturated with water for more than a few days and less than 20% organic carbon by weight; or

(2) saturated with water for long periods or artificially drained and has the following proportions of organic carbon:

(a) less than 18% organic carbon by weight, if 60% or more of the mineral fraction is clay;

(b) less than 12% organic carbon by weight, if the mineral fraction has no clay; or

(c) a proportional content of organic carbon between 12% and 18% if the clay content of the mineral fraction is between 0 and 60%.

Soil material that has more organic carbon than the amounts given above is considered to be organic. Organic soil material is defined as follows:

(1) never saturated with water for more than a few days and 20% or more organic carbon; or

(2) saturated with water for long periods or artificially drained and, excluding live roots, has the following proportions of organic carbon:

(a) 18% or more organic carbon if the mineral fraction is 60% or more clay;

(b) 12% or more organic carbon if the mineral fraction has no clay; or

(c) a proportional content of organic carbon between 12% and 18%, if the clay content of the mineral fraction is between 0 and 60%.

Number 1 in this latter definition is intended to include what have been called litter or organic horizons. Number 2 covers materials that have been called peat and muck. Not all organic materials accumulate in or under water. Leaf litter may rest on a lithic contact and support a forest or a fen. The only soil type present in these situations is organic. The mineral fraction is appreciably less than half the weight and is only a small percentage of the volume of the soil.

Herbaceous wetlands on mineral soil are usually termed "marshes" or "wet meadows" (Moss 1955; Daubenmire 1968). Literature on Rocky Mountain vegetation applies the terms "meadow" and "wet meadow" to so many types of vegetation and different ecological situations that a precise definition of meadow is not possible. Generally, meadows occur in seasonally-flooded basins and flats, and soils are usually not wet during the entire growing season. It is obvious that wetlands dominated by <u>Erigeron peregrinus</u>, such as those occurring in

Rocky Mountain National Park (Wilson 1969), do not satisfactorily fit the concept of marsh, because marshes characteristically are dominated by grasses, sedges, and rushes, rather than forbs.

At this time it seems best to leave all options open and use marsh as the term for mineral soil herbaceous wetlands on the wettest side of the water gradient and wet meadows as the drier end of the moisture gradient. It seems that marshes are usually associated with a permanent water source, have a water table close to the surface (Tansley 1939), and have water for one or more months during the growing season, whereas wet meadows have surface water a small part of the growing season (Moss 1955), up to a few weeks long (Dix and Smeins 1967), and are associated with late-lying snowbeds, ephemeral springs, and other sources.

Herbaceous wetlands that occur on organic soils are either fens or bogs. Worldwide, the two main classes of peatlands (mires) are ombrotrophic bogs and minerotrophic fens (Schwintzer 1978). According to Heinselman (1963), the degree of isolation from mineral-influenced groundwater is the key to understanding floristic patterns in Minnesota peatlands. He found that surface of fens has water available to seedlings and sporelings that has been in contact with mineral soil and thus has a much better supply of nutrients than is contained in rainwater. Similar patterns in boreal peatlands also occur in Canada and Scandinavia (Sjors 1961, 1965). Bogs, in contrast to fens, have water available to seedlings and sporelings that has scarcely more nutrients than are available in rainwater, approximately 12 to 18 ppm electrolytes, with an electrical conductivity of 0.02 to 0.03 µmho/cm (Daubenmire 1968). Direct precipitation is the main water source for bogs, and the water is deficient in calcium and other telluric minerals (ions leached from mineral soils and bedrock by percolating water). Humic acids are always formed in peatlands, and the scarcity of metal ions in precipitation (except in maritime areas) leads to strongly acid reactions of water and peat in ombrotrophic peatlands (Sjors 1959).

Bogs can develop from fens when the germination surface of the peat becomes elevated enough so that rain keeps the surface peat leached. In this situation, ombrotrophic peat develops over eutrophic peat (Tansley 1939). A decline in calcium and an increase in acidity lessens the availability of nitrogen and phosphorus in the bog peat (Daubenmire 1968). A Sphagnum mat develops and may grow upward and outward fast enough to smother many slow-growing plant species.

Fens are typically dominated by sedges and other graminoids, whereas bogs usually have a moss layer dominated by Sphagnum spp. Fens may also have an abundant moss layer, but these species are more exacting in their nutrient requirements. Bogs are usually called "moss" (or mosse) in Sweden (Sjors 1950) and elsewhere in Europe (Tansley 1939); the term describes the characteristic abundance of mosses. Sjors (1950) presents a figure relating types of fens and bogs to pH of their water source (Figure 33). The pH of bog (moss in Figure 33) water generally ranges from 3.5 to 4.3. Fens range from extremely rich, with pH 7.0 to 8.5, to extremely poor, with pH 3.7 to 5.2. Sjors also classified four other types of fens, based on floristic richness, between the extremes (Figure 33). Fens are generally circumneutral in reaction and are species rich (Sjors 1959). Extremely rich fens have a high calcium content and abound with calciphilous plant species.

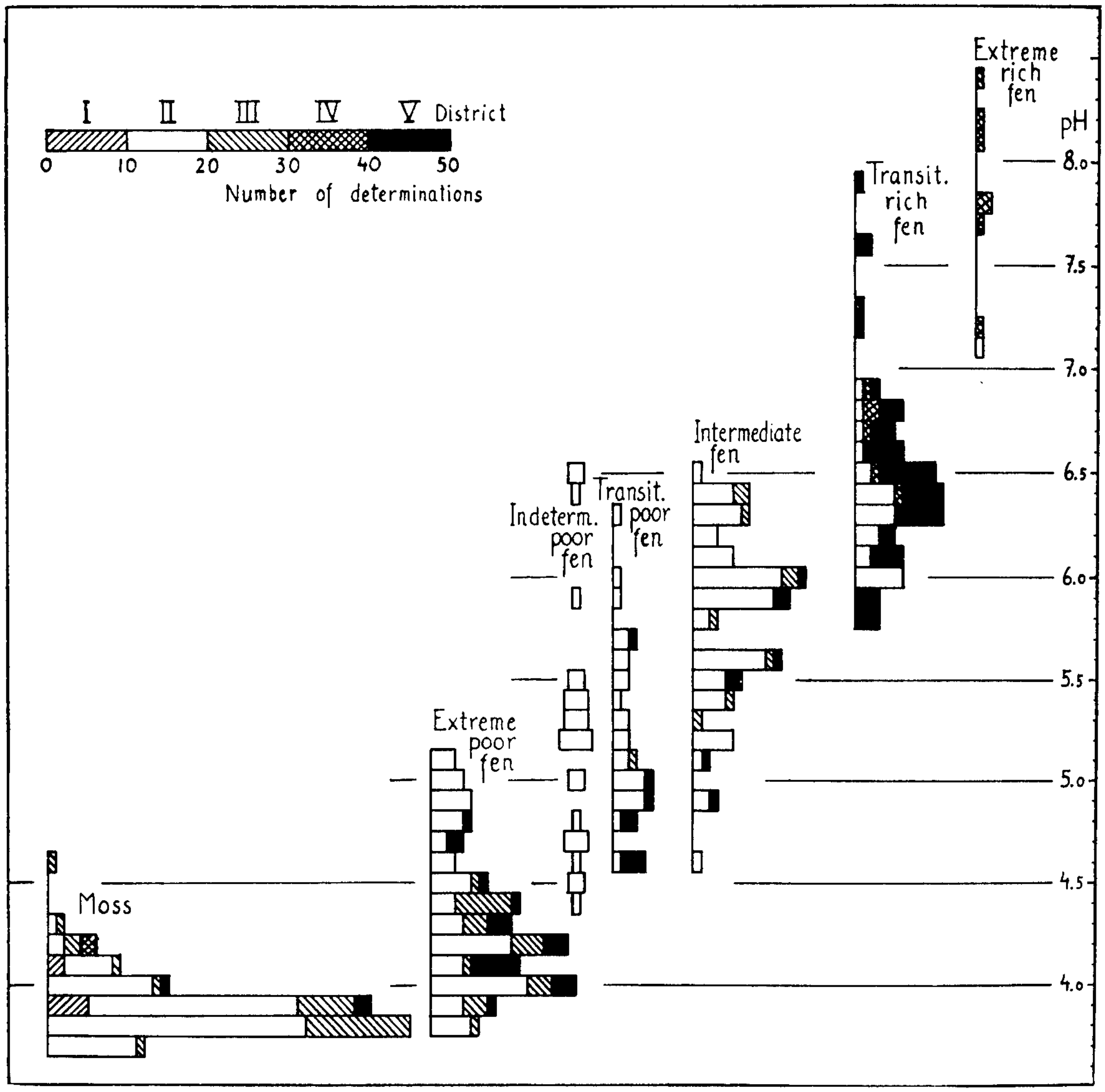


Figure 33. Distribution of pH values in water from different kinds of mire communities in North Sweden. (From Sjors 1950.)

The term "carr" has been used in a number of different ways. For example, Tansley (1939) defines carrs as fens with a dominance of shrubs. In the Rocky Mountains, carr has been used to describe shrub-dominated wetland vegetation on organic and mineral soils (Phillips 1977; Hallock 1985) including streamside vegetation. Dix (1974) considers carrs to be dependent for minerals upon frequent flooding by fast-moving streams; however, shrub wetlands are abundant on uplands underlain with possible permafrost, such as on Guanella Pass in Colorado's Front Range, and elsewhere near treelimit where there are no streams. In the present classification, we use the term carr as Tansley did, for shrub-dominated fens. Shrub-dominated vegetation on organic ombrotrophic soils is termed shrub-dominated bog.

Shrub-dominated wetland vegetation on mineral soil is called shrub wetlands, for lack of a better term. This includes shrub wetlands with either fresh or saline water sources.

Forests dominated by both broadleaf deciduous and coniferous tree species that occur in uplands away from the influence of streams are treated in this section as forested wetlands.

Swamps have a water level that is above the soil surface all summer (Tansley 1939) and, in some definitions, trees cover at least 25% of the ground (Zoltai et al. 1975). According to this definition, no true swamps are known to occur in the Rocky Mountains. The only Rocky Mountain wetlands that might resemble this wetland type are emergent wetlands, discussed under permanent shallow standing-water communities, in which spruce (Picea engelmannii), subalpine fir (Abies lasiocarpa), and lodgepole pine (Pinus contorta) or aspen (Populus tremuloides) have become established. Tree species such as Picea mariana and Larix laricina occur in bogs in Canada and Alaska but do not grow in the Rocky Mountain region. In southeastern Alaska, Pinus contorta is abundant in wetlands and while this is the most common tree species in many Rocky Mountain wetlands it generally is not abundant or vigorous.

a. Fens. Fens are dominated primarily by species of Carex, Juncus, Eleocharis, Deschampsia, and Calamagrostis and occur on relatively flat, constantly wet valley bottoms (Figure 34). According to Fuller (1930), Illinois and Colorado fens are dominated by similar species. Many of the most common fen dominants, such as Carex utriculata, C. aquatilis, Eleocharis palustris, and many others, have a circumpolar boreal and temperate zone distribution. Mosses may be abundant but seldom include Sphagnum spp. In western Alberta, Canada, Campylium stellatum is the most important moss in the

Figure 34. Permanently wet subalpine fen in Paradise Park, 3,196 m (10,480 ft) elevation, Rocky Mountain National Park, Colorado. (Photo by B. E. Willard.)

driest flarks (flarke, in German; rimpi in Finnish; means the hollow between raised strings) in minerotrophically rich fens, while Tomenthypnum nitens is the most important and widespread species of strings (Slack et al. 1980). These combinations of flarks and strings, also called strangmoors, are common in wetlands in the sub-Arctic. This patterned ground occurs in some Rocky Mountain fens, as can be seen in Figure 35. The only palsas known from the conterminous U.S. are from a fen on the Beartooth Plateau of Wyoming (Collins et al. 1984). In the wettest habitats in the Rocky Mountains, rhizomatous species of Carex, such as C. utriculata, C. aquatilis, C. siccata, C. hoodii, C. nebraskensis, C. languinosa, C. vesicaria, and C. canescens can dominate communities.

Vegetation of fens with a very high water table may consist of a single vascular plant species, such as Carex utriculata, which forms a dense and continuous mat. Communities dominated by Carex utriculata are reported mostly from the Lower and Upper Montane or lower Subalpine Zones in the Rocky Mountains, but also occur in the foothills down to the plains. Wilson (1969) found that C. utriculata usually dominates the wettest, most deeply and persistently flooded sites in Colorado's Rocky Mountain National Park, such as filled-in glacially derived lakes. Communities dominated by this species are reported for Grand Lake and Lake John, Colorado (Johnson 1941), northern Colorado (Ramaley 1919), and Crested Butte, Colorado (Langenheim 1962). Associated species include Carex canescens, C. vesicaria, C. languinosa, C. aquatilis, C. festivella, C. siccata, C. hoodii, C. nebraskensis, C. praegracilis, Juncus longistylus, J. saximontana, J. balticus, Agrostis alba, and others. In Colorado's Cross Creek Valley, stands dominated by C. utriculata occur in habitats with a water table at an average of 15 cm (5.9 in)

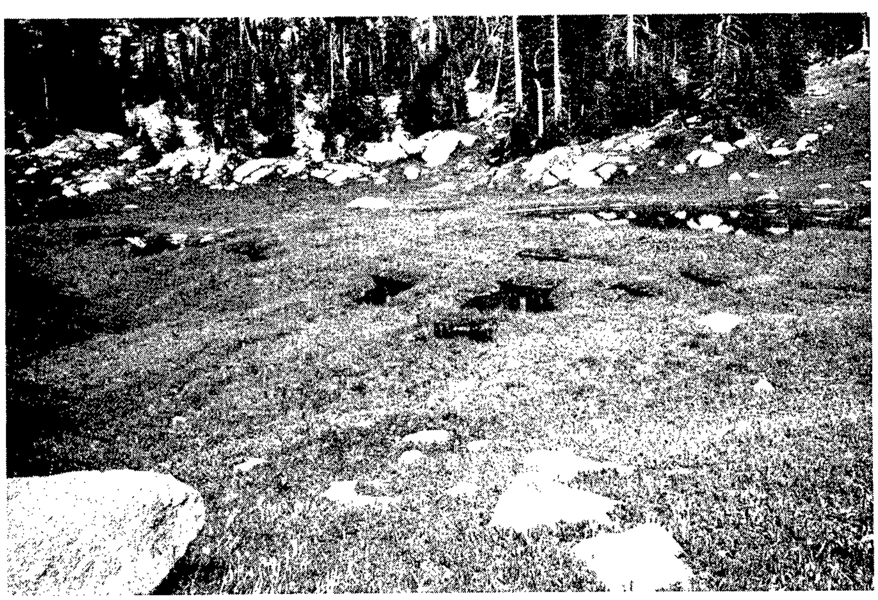


Figure 35. Strings and hollows (flarks) in fen, 10 Lakes Park, 3,431 m (11,250 ft) elevation, Rocky Mountain National Park, Colorado. (Photo by B. E. Willard.)

below the ground surface (Figure 36) (Cooper 1986). Around Candle Lake, Saskatchewan, Canada, Carex utriculata ranges from soil with a water table at 80 cm (32 in) below the ground surface to 60 cm (24 in) of standing water, but is most abundant in 1 to 19 cm (1.4 to 7.5 in) of standing water (Jeglum 1971). On the Big Piney Ranger District in the Bridger-Teton National Forest in Wyoming, C. utriculata dominates stream bottoms from the main stream edge to the valley edge (Mutz and Graham 1982). Soils are Cumulic Cryoborolls, wet at 50 cm (20 in), with a water table at 68 cm (27 in). Production of Carex utriculata communities is 465 g/m² in southern Michigan (Getz 1960) and 420 g/m² in England (Pearsall and Gorham 1956). Similar values are to be expected in the Rocky Mountains. Table 13 compares the composition of C. utriculata stands.

A clay pan may form in soils of Carex aquatilis-dominated fens in Rocky Mountain National Park (Wilson 1969). This raises the water table and initiates allogenic successional processes, allowing Carex utriculata to take over these sites. The Carex utriculata fens sampled by Wilson (1969) had an average of 41% organic matter in the soil profile. There was an average of three species in the 16 stands sampled; vascular plant cover averaged 27%; pH in the top 20 cm (8 in) of soil was 4.5; and 6.1 grams of calcium occurred per cubic centimeter of soil.

Figure 36. Zonation of fens in Cross Creek Valley, Sawatch Range, Colorado. Pond in center of photograph is surrounded by a Carex utriculata fen, and in foreground is a Calamagrostis canadensis fen. (Photo by D. J. Cooper.)

Table 13. Comparative stand data for Carex utriculata-dominated communities.

Species	Abundance categories[a]: Mutz and Graham (1982)		Wilson (1969)		Cooper (1986)	
Carex utriculata	74	94	75	95	75	95
Carex aquatilis	22	21	3	0	15	0
Deschampsia caespitosa	10	0.1	0	0	0	0
Geum macrophyllum	30	0	0	0	0	1
Polemonium occidentalis	17	0	0	0	0	0
Poa pratensis	5	0	0	0	0	0
Castilleja miniata	3	0	0	0	0	0
Carex microptera	3	0	0	0	0	0
Calamagrostis canadensis	0	2	0	7	0	0
Viola canadensis	0	0.1	0	0	0	0
Sphagnum platyphyllum	0	0	0	20	0	5
Carex canescens	0	0	0	0	10	0
Drepanocladus exannulatus	0	0	0	15	15	0
Caltha leptosepala	0	0.4	0	0	0	0
Aulacomium palustre	0	0	0	5	0	0
Calliergon stramineum	0	0	0	5	0	0
Viola episila ssp. repens	0	0	0	0	0	0

[a]Wilson's data are mean frequency values for two stands. Cooper's data are percent canopy coverage from sample numbers 85-41 and 85-55. Mutz and Graham's data are average percent coverage for two stands.

Two types of fen communities occur in Rocky Mountain National Park's Big Meadows (Bierly 1972), which is in the Montane Zone at 9,200 ft elevation. At the wettest end of the moisture gradient, Carex aquatilis, C. rostrata, Caltha leptosepala, and Eleocharis pauciflora were dominants. This community type is poor in vascular plant species, but mosses are abundant. The water table averaged 39.5 cm (15.6 in) deep in late summer and soils had low bulk density, high cation exchange capacity, and a low calcium to magnesium ratio. Bierly felt that this community was nearly ombrotrophic. In landscape depressions, where sluggish drainage occurs, peat averaged 25 cm (9.9 in) in depth and Carex aquatilis, Potentilla gracilis, Galium brandegei, Stellaria laeta, Calamagrostis canadensis, Deschampsia caespitosa, and Pleurocarpous mosses were abundant.

Carex aquatilis communities occur throughout the Rocky Mountains in both the Montane and Subalpine Zones (Table 13) and often are intermediate between the wetter fens dominated by Carex utriculata and more mesic fens with Calamagrostis canadensis (Wilson 1969; Cooper 1986). Carex aquatilis is usually represented by subspecies stans in the Subalpine Zone and subspecies aquatilis in the Montane Zone (Wilson 1969).

The *Carex aquatilis* stands described by Hess (1981) from the Roosevelt and Arapahoe National Forests in Colorado (Table 14) occur on nearly level terrain that is poorly drained. This was the most hydric of all Subalpine associations he described. Deep peat accumulates due to the hydric environment. Soils are Typic Cryohemists, and Typic Cryosaprists. Depth to water table varied from 30 cm (11.8 in) in the wettest stands to greater than 1 m (3.3 ft) in the driest stands. Organic matter had a pH of 6.0 to 6.4. In Colorado's Cross Creek Valley, *Carex aquatilis* communities occur in a wide variety of situations, some with standing water and others with a deep water table (Cooper 1986). In Rocky Mountain National Park (Wilson 1969), *Carex aquatilis* communities occur on soils with an average of 50% organic matter. Soil pH of the top 2 dm averages 4.4 and analyses show an average of 6.3 g of calcium per cubic dm. The fens described by Wilson (and probably Cooper 1986) would be extremely poor fens according to Sjors (1950) (Figure 33), whereas Hess' stands would be intermediate fens.

Table 14. Comparative stand data for *Carex aquatilis*-dominated communities.

Species	Abundance categories[a]			
	Wilson (1969)	Hess (1981)	Cooper (1985)	
Carex aquatilis	95.4	38 (100)	95	95
Carex utriculata	44.3	22 (100)	0	0
Carex canescens	0	1 (75)	0	0
Calamagrostis canadensis	21.4	0	0	5
Deschampsia caespitosa	0	1 (100)	0	0
Eleocharis pauciflora	1.3	23 (100)	0	0
Viola canadensis	7.6	0	0	0
Epilobium anagalladifolium	6.7	0	0	0
Galium trifidum	15.3	0	+[b]	0
Pedicularis groenlandicum	4.6	3 (75)	0	0
Sedum rhodanthum (*Clementsia rhodantha*)	1.7	1 (50)	0	0
Caltha leptosepala	0	8 (75)	0	0
Erigeron peregrinus	0	+ (50)	0	0
Veronica wormskjoldii	0	+ (50)	0	0
Cardamine cordifolia	0	0	15	0
Rorippa teres	0	0	1	0
Viola episila ssp. *repens*	0	0	10	0
Aulacomium palustre	0	0	5	0
Plagiomnium elliptica	0	0	1	0

[a]Wilson's data (1969) are mean frequency values for seven stands. Hess' data (1981) are average percent canopy coverage (constancy) for four stands. Cooper's data (1986) are percent canopy coverage for sample numbers 85-49 and 85-45. Constancy is the percentage of sampled stands which contain a species.

[b]+ = presence, <1% coverage.

At 2,500 m (8,202 ft) elevation in the Montane Zone of Colorado's Front Range, Carex aquatilis grows on the coolest soils that occur; they have an average July temperature of 19 °C (66.2 °F) (Chapin 1981). On warmer soils in the same area, where an average July temperature of 22 °C (71.6 °F) occurs, Scirpus spp. and Eriophorum angustifolium are dominant; on the warmest wetland soils, Eleocharis spp. and Typha latifolia grow. species form tight zones in wetlands along a water depth gradient. Carex aquatilis clearly has an ability to deal with low soil temperatures. Temperature range for C. aquatilis in Colorado is similar to the range for Typha latifolia in Alaska, demonstrating that even though average summer temperatures of communities are different in Alaska and Colorado, the position of communities along the temperature gradient is similar in both areas.

Carex aquatilis dominates two different societies of the Montane-Subalpine Moor Association of Ramaley (1919) around northern Colorado lakes. In the Montane Zone, Carex vesicaria, C. languinosa, C. canescens, C. illota, C. lasiocarpa, C. athrostachya, C. disperma, C. aurea, and C. paupercula occur, and in the Subalpine Zone C. scopulorum, C. nigricans, C. nelsonii, C. chalciolepis, and C. capillaris grow. Carex aqualities also dominates a Subalpine Half-submerged Carex Association, which occurs at the inlets and outlets of lakes (Ramaley 1919), but this latter association should be classified as emergent vegetation, not fen, since permanent standing water occurs and soils are probably not organic. In other parts of Colorado, Ramaley (1920) described a moor around subalpine lakes as characterized by Carex aquatilis, Sedum rhodanthum, Ligusticum tenuifolium, and Salix glauca. In Colorado's San Juan Mountains, Carex aquatilis dominates stands where water depth is from 25 cm (9.9 in) above the soil surface to 30 cm (11.8 in) below the soil surface (Keammerer and Keammerer 1983); also occurring are Deschampsia caespitosa, Caltha leptosepala, Bistorta bistortoides, Calamagrostis canadensis, Carex canescens, Eleocharis macrostachya, and Phleum commutatum.

Carex lanuginosa dominates a Plains-foothills Sedge Moor Association described by Ramaley (1919); also occurring are Carex nebraskensis, C. aquatilis, C. utriculata, C. canescens, C. stipata, C. lasiocarpa, C. vesicaria, and C. athrostachya. Carex languinosa dominates sod-forming communities near open water, with no erosion or deposition, near Jackson Hole, Wyoming (Reed 1952); also prominent were C. nebraskensis, C. occidentalis, and Eleocharis macrostachya. Carex lanuginosa dominates Montane Zone wetlands in Colorado's Front Range (Mutel 1973) at the driest end of the wet meadow gradient. Carex languniosa also dominates wetlands in the vicinity of Creede, Colorado (Stewart 1940). Carex lasiocarpa is common in western Montana and Idaho and probably dominates wetlands communities in those areas.

Mutz and Graham (1982) describe a Carex simulata community (Table 14) from the Big Piney Ranger District in Wyoming. Carex simulata dominates a dense turf in which Carex utriculata, C. aquatilis, and C. nebraskensis are also abundant. The stands occur in valley bottoms in abandoned stream channels filled with organic matter. Soils are mostly Histic Cryaquoll or Aquic Cryoborolls, but one stand occurs on a Cryaquent. Mosses are common, and it was noted that Carex simulata can outcompete other species in saturated soils, although it may do better in more well-drained habitats than those in which it normally grows. Productivity averaged 184.6 g/m², ranged from 91 to 254 g/m², and was mostly from graminoids.

Carex simulata dominates the open fen association in the Pine Butte Fen, Montana (Lesica 1982) (Table 14). These stands would be classified as rich fens according to Sjors (Figure 33). They are associated with poorly drained fibrous peat of the Dougcliff Soil Series. The peat surface displays string and flark patterns, and flarks contain standing water most or all of the growing season. Strings are dominated by Carex simulata, C. aquatilis, Juncus balticus, and Campylium stellatum, and flarks by Utriculata vulgaris, Utricularia minor, Menyanthes trifoliata, and Scorpidium scorpioides. The Scirpus acutus phase occurs in patches throughout the Pine Butte Fen (samples numbers 2, 5, and 9 in Table 15). Carex simulata is occasionally locally abundant, but usually sporadic in wet areas of the Rocky Mountains, occurring from Montana to New Mexico (Hermann 1970).

The Carex nebraskensis - Alopecurus alpinus type fen occurs in wetlands of the Big Hole National Battlefield, Montana (Pierce 1982). Carex eleocharis dominates wetlands around Aldrich Lake, Colorado (Johnson 1941). Carex scopulorum dominates wetlands along creeks and streamlets in the high Subalpine Zone as well as being typical of common alpine wetlands of Colorado's Front Range (Komarkova 1979; Willard 1979).

Several species of Eleocharis can dominate fens or emergent communities in the Rocky Mountains, including E. pauciflora (E. quinqueflora), E. palustris, E. macrostachya, and E. acicularis. Eleocharis pauciflora dominates fens on the deepest peat, 40 to 125 cm in depth, in Colorado's Rocky Mountain National Park (Wilson 1969). Table 16 presents Wilson's data, which are derived from 15 stands. There was an average of 15 species per sampled stand. Soils were composed of 66% organic matter, and the top 2 dm (7.9 in) had a pH of 4.3, with 4.1 g/dm³ of calcium. Soils also had the lowest bulk density of all communities described by Wilson, 268 g/dm³ (top 2 dm of soil). Hydrarch succession may lead from this community to communities dominated by Caltha leptosepala when the water table is lowered to just below the ground surface in summer, and then to Erigeron peregrinus when it is lowered even further. Succession such as this is not inevitable, however, and each community is represented by stable and successional vegetation.

Juncus balticus (J. arcticus) dominates a wide variety of fen communities all over the Rocky Mountains in both the Montane and Subalpine Zones (Table 17; Figure 37). Other important Juncus spp. include J. parryi and J. mertensianus, which are characteristic of high Subalpine wetlands.

Mutz and Graham (1982) describe Juncus balticus stands as being small, near surface water sources (i.e., ephemeral creeks, permanent streams, or beaver ponds, within 6 dm of water surface), and with Cryobolls or Cryaquolls soils. Productivity averaged 356.2 g/m² and ranged from 222 to 588 g/m², mostly from graminoids. In the Big Hole National Battlefield, Montana, Juncus balticus has increased in cover since grazing began in 1877, and previously may not have been abundant (Pierce 1982). Soils were relatively dry in August,

Table 15. Comparative stand data for *Carex simulata*-dominated communities.

	Mutz and Graham (1982)	Lesica (1982)					
Stand number	-	1	4	8	2	5	9
Conductivity (µmho/cm)	-	445	520	600	440	490	430
pH	-	7.0	7.1	7.2	7.2	7.1	7.1
Species	Average percent cover and (constancy on 10 point scale)	Prominence values					
Carex simulata	78/(10)	250	250	210	38	76	27
Carex aquatilis	4/(7)	250	1	40	22	0	1
Scirpus acutus	0	0	0	0	286	268	256
Carex nebraskensis	11/(3)	0	0	0	0	0	0
Carex utriculata	10/(8)	0	0	0	0	0	0
Carex livida	0	17	9	12	5	6	15
Carex limosa	0	1	52	0	34	113	7
Eleocharis pauciflora	0	2	53	25	68	13	1
Muhelnbergia glomerata	0	25	13	1	3	5	15
Deschampsia caespitosa	1/(8)	0	0	0	0	0	0
Aster foliaceous	3/(3)	0	0	0	0	0	0
Equisetum laevigatum	4/(2)	0	0	0	0	0	0
Pedicularis groenlandicum	+/(7)[a]	0	0	0	0	0	0
Poa pratensis	+/(7)	0	0	0	0	0	0
Menyanthes trifoliata	0	279	29	0	136	1	0
Utriculata vulgaris	0	0	0	67	9	11	65
Utriculata minor	0	49	4	1	7	2	11
Aster junciformis	0	7	4	4	18	2	1
Galium boreale	0	42	1	0	64	27	1
Triglochin maritimum	0	20	155	151	10	1	7
Pentaphylloides floribunda	0	65	18	21	117	14	20
Betula glandulosa	0	26	26	1	26	33	34
Salix candida	0	2	2	1	2	2	1
Drepanocladus revolvens	0	174	80	17	146	55	0
Scorpidium scorpioides	0	60	25	0	51	29	92
Campylium stellatum	0	178	320	145	206	204	132

[a]+ = presence, <1.

Table 16. Stand data for Eleocharis pauciflora-dominated community. (From Wilson 1969.)

Species	Mean frequency
Eleocharis pauciflora	99.2
Carex utriculata	1.3
Carex aquatilis	78.1
Caltha leptosepala	12.5
Carex illota	3.5
Deschampsia caespitosa	3.9
Viola canadensis	8.1
Erigeron peregrinus	3.1
Podagrostis sp.	1.4
Epilobium anagalladifolium	7.5
Pedicularis groenlandicum	19.9
Sedum rhodanthum (Clementsia rhodantha)	10.7

but other times mottled or very wet and not saline. Mutz and Graham (1982) also report that Juncus balticus may be unpalatable and increase with grazing. Hess (1981) described his Juncus balticus - Carex spp. habitat type as occurring on poorly-drained low-lying to concave landscapes between 2,000 and 2,400 m (6,562 - 7,874 ft) elevation in north-central Colorado. Soils were organic, Typic Borosaprists, moist for the entire growing season, and water-saturated for a significant part of the growing season. Soils had a pH of between 5.6 and 6.2, and were dark and mottled. The presence of Taraxacum officinale indicates extensive human disturbance, such as livestock grazing, and these stands may represent zootic climaxes.

Grass-dominated fens in the Rocky Mountains may be tall in stature, due to the height of Calamagrostis canadensis and Deschampsia caespitosa, the two most abundant species. Abandoned beaver ponds dominated by these two species of grasses support more productive vegetation than active ponds (Neff 1957). Calamagrostis canadensis-dominated communities occur on silty "bog" soils in Rocky Mountain National Park (Wilson 1969). There was an average of 15 species of vascular plants per stand, and soils had an average of 41% organic matter. Soils had pH of 4.5 in the top 2 dm (7.9 in), and contained 8.5 g/dm^3 of calcium. A typical soil profile for a Calamagrostis canadensis fen is shown in Table 18. Wetlands dominated by Calamagrostis canadensis occur throughout the Rocky Mountains usually at higher elevations, but well below treelimit (Table 19).

Table 17. Stand data for *Juncus balticus*-dominated communities.

Species	Average percent coverage (constancy): Mutz and Graham (1982)[a]	Hess (1981)[b]
Juncus balticus	67 (10)	56 (100)
Carex douglasii	8 (3)	0
Carex nebraskensis	5 (2)	9 (75)
Carex praegracilis	4 (5)	4 (50)
Carex utriculata	3 (2)	0
Carex festivella	0	2 (100)
Carex lanuginosa	0	1 (75)
Deschampsia caespitosa	2 (10)	5 (100)
Calamagrostis canadensis	0	+ (75)[c]
Eleocharis acicularis	0	7 (50)
Eleocharis rostellata	0	+ (75)
Poa pratensis	1 (10)	6 (100)
Phleum alpinum	1 (8)	0
Phleum pratense	0	2 (100)
Achillea millefolium	1 (7)	2 (100)
Allium geyeri	0	+ (50)
Aster eatonii	1 (2)	0
Aster foliaceus	4 (8)	0
Dodecatheon pulchellum	0	+ (100)
Fragaria virginica	11 (7)	0
Geum trifidum	2 (2)	0
Potentilla gracilis	4 (8)	0
Pentaphylloides floribunda	0	2 (100)
Ribes inerme	0	+ (50)
Taraxacum officinale	1 (3)	2 (100)
Trifolium repens	0	8 (50)

[a]Mutz and Graham (1982) use a 10-point constancy scale and their data are from six stands in the Grey's River region of western Wyoming.

[b]Hess (1981) uses percentage constancy, and his data are from four stands.

[c]+ = presence, <1.

Figure 37. Juncus balticus fen at 3,050 m (10,000 ft) elevation in South Park, Colorado. (Photo by B. E. Willard.)

Table 18. Soil profile for a Calamagrostis canadensis fen community. (From Wilson 1969.)

Horizon	Depth cm	Texture	Structure	Color	Mottling
A	0-10	silty	crumbly	brown-black	no
A-B	10-28	clayey	blocky	brown-black	yes
B	28-48	clay	blocky	brown	yes
	48-56	clayey sand	single grain	red-brown	yes
B-C	56-69	clay with charcoal	blocky	brown	yes
Cg	69-70	clay	massive	gray-rust	yes
Bedrock	70+				

Table 19. *Calamagrostis canadensis* fen community samples.

Species	Abundance			
	Wilson (1969)[a]	Cooper (1986)[b]		
Calamagrostis canadensis	90.1	95	85	60
Carex aquatilis	83.3	0	0	0
Carex utriculata	18.4	0	0	0
Caltha leptosepala	7.8	0	0	0
Deschampsia caespitosa	10.6	0	0	0
Viola canadensis	42.2	0	0	0
Erigeron peregrinus	4.1	0	0	0
Senecio sp.	7.0	0	0	0
Bistorta bistortoides	1.8	0	0	0
Epilobium angustifolium	16.3	0	0	0
Poa reflexa	7.3	0	0	0
Veronica sp.	5.9	0	0	0
Taraxacum officinale	3.3	0	0	0
Hordeum jubatum	1.1	0	0	0
Poa pratensis	4.4	0	0	0
Galium trifidum	14.6	+[c]	0	3
Pedicularis groenlandicum	1.4	0	0	0
Senecio triangularis	13.4	0	0	0
Trisetum wolfii	1.9	0	0	0
Geum macrophyllum	0	5	0	1
Stellaria longifolia	0	+	0	+
Cardamine cordifolia	0	1	5	0
Salix drummondiana	0	0	0	20
Heracleum sphondylium	0	0	0	30
Mertensia ciliata	0	0	0	15
Epilobium lactiflorum	0	0	0	+
Thalictrum sparsiflorum	0	0	0	2

[a]Wilson's data are from nine stands and are mean frequency.

[b]Cooper's stands are numbers 85-34, 85-43, and 85-40, and data are coverage.

[c]+ = presence, <1.

In Colorado's Cross Creek Valley (Cooper 1986), Calamagrostis canadensis forms tussocks, and where the tussocks fuse, it may produce highly organic soils.

Deschampsia caespitosa-dominated fens (Table 20) are more sporadic in occurrence, but may contribute the greatest primary production of any species on poorly-drained high-elevation valley bottom wetlands flooded by snowmelt in western Montana (Mueggler and Stewart 1980) and in the Colorado Front Range (Komarkova 1979). This grass grows especially densely in the Deschampsia caespitosa/Carex spp. habitat type in Montana, and on flood-irrigated pastures in Colorado's Middle and North Parks. Deschampsia stands occur where they have 0.76+ m (2.5+ ft) of winter snow cover (Komarkova 1979; Willard 1979).

Table 20. Stand data for a Deschampsia caespitosa/Caltha leptosepala fen community. (From Hess 1981.)

Species	Cover (constancy)
Deschampsia caespitosa	51/(100)
Calamagrostis canadensis	4/(50)
Carex aquatilis	4/(100)
Carex utriculata	+/(50)[a]
Eleocharis rostellata	+/(50)
Phleum alpinum	1/(100)
Caltha leptosepala	22/(100)
Epilobium lactiflorum	+/(50)
Erigeron glabellus	+/(50)
Erigeron speciosus	+/(50)
Pedicularis groenlandicum	1/(75)
Bistorta bistortoides	5/(75)
Potentilla diversifolia	+/(50)
Ranunculus alismaefolius	2/(50)
Sedum rhodanthum (Clementsia rhodantha)	2/(75)
Senecio crocatus	+/(50)
Veronica wormskjoldii	1/(50)

[a]+ = presence, <1.

Hess (1981) described two Deschampsia-dominated community types; one occurs in the Alpine Zone--Deschampsia caespitosa- Geum rossii community; the other--Deschampsia caespitosa - Caltha leptosepala community (Table 20)--occurs on level terraces, with high snow accumulation caused by topographic position. Soils are mineral, but have high organic matter content. Soils are classified as Inceptisols and have Umbric or Histic Epipedons with pH in the A horizon of 5.2 to 5.4. Subalpine stands occur on wet to mesic subalpine sites at 2,900 to 3,350 m (9,515 to 10,991 ft) elevation. Deschampsia-dominated communities have been reported by Bonham and Ward (1970), and a Deschampsia caespitosa - Carex nebraskensis meadow type is described by the Soil Conservation Service (1978).

Wilson (1969) described two herb-dominated wetlands, from Rocky Mountain National Park, Colorado, that have highly organic soils and, for now, are grouped with fens, even though they are clearly different and not dominated by graminoids (Table 21). Twelve stands, dominated by Caltha leptosepala, had soils with an average of 46% organic matter, and eight stands, dominated by Erigeron peregrinus, similar to Figure 54, had 36% organic matter. Both are species-rich community types, with the Caltha community averaging 20 vascular plant species, and the Erigeron community 27 species.

Table 21. Stand data from communities dominated by Caltha leptosepala and Erigeron peregrinus. (From Wilson 1969.) Listed are the most abundant and characteristic species.

Species	Mean frequency	
	Caltha	Erigeron
Caltha leptosepala	85.5	61.4
Erigeron peregrinus	38.8	75.5
Senecio sp.	78.8	67.3
Viola canadensis	22.7	49.3
Arnica sp.	11.6	43.5
Carex nigricans	49.1	22.1
Carex aquatilis	69.7	36.5
Carex illota	29.8	2.6
Deschampsia caespitosa	62.3	52.9
Calamagrostis canadensis	1.7	20.4
Podagrostis "small"	14.2	6.4
Podagrostis sp.	2.5	23.9
Pedicularis groenlandicum	30.1	16.0
Veronica wormskjoldii	9.0	15.7
Poa reflexa	8.4	35.9
Epilobium sp.	17.8	53.9
Bistorta bistortoides	8.9	23.4
Eriophorum angustifolium	0	8.6
Trisetum wolfii	6.3	12.9
Senecio triangularis	3.8	10.6

b. Bogs. No true ombrotrophic bogs from the Rocky Mountains south of Canada are described in the literature. They probably occur very seldom because succession from formation of minerotrophic peat to formation of oligotrophic peat (fen to bog) occurs very seldom. This succession is interrupted by fire or floods (Phillips 1977), which rework floodplains. Also, low precipitation (Bierly 1972) and high evapotranspiration limits downward leaching. A good example of a *Sphagnum* mat encroaching upon a *Carex* fen occurs in Paradise Park, Rocky Mountain National Park (Figure 38), but floristic and soil details are not yet known. The most common *Sphagnum* in Colorado, *S. warnstorfii*, has strongly minerotrophic ecological requirements.

Figure 38. Very wet fen, on left side of photograph, is being encroached upon by *Sphagnum* spp. mat, at right. Paradise Park, 3,187 m (10,450 ft) elevation in Rocky Mountain National Park, Colorado. (Photo by B. E. Willard.)

Typical bogs in the Northern Hemisphere are characterized floristically by a mat of *Sphagnum* spp. and members of the vascular plant family Ericaceae growing in the mat. Very few members of the Ericaceae occur in the southern Rocky Mountains due to the continental climate and blockage to their southward migration by the arid Red Desert basin in southern Wyoming (Weber 1965). The following 15 plant species have been termed characteristic of North American bogs by Transeau (1903): *Menyanthes trifoliata*, *Dulichium arundinaceae*, *Potentilla palustre*, *Scheuchzeria palustre*, *Eriophorum angustifolium*, *Drosera rotundifolia*, *Sarrocenia purpurescens*, *Oxycoccus palustris*, *Gaultheria hispula*, *Andromeda polifolia*, *Chamaedaphne calyculata*, *Ledum palustre* ssp. *groenlandicum*, *Kalmia polifolia* ssp. *microphylla*, *Betula pumila*, and *Larix laricina*. Of these species, *Potentilla*, *Menyanthes*, *Eriophorum*, *Drosera*, and *Kalmia* occur in the Rocky Mountains, but all are considered rare.

Kalmia polifolia ssp. microphylla is abundant locally in a heath community around lakes in north-central Colorado (Ramaley 1920), and a localized small sedge-moss community type in Colorado's Front and Sawatch ranges (Willard 1985), but whether these are true bogs is not known. Eriophorum angustifolium occurs occasionally and sporatically in wet Subalpine fen peats; E. scheuchzeri, E. chamissonis, and E. gracile grow in fens in a few places in Colorado and may be expected in other parts of the Rockies. Menyanthes trifoliata is found along the edge of a few ponds in Rocky Mountain National Park (Nelson 1970; Willard 1985).

One complex of wetlands, called the Keystone Bog, in the West Elk Mountains of Colorado, occurs along a fault zone from which iron-rich, acidic water seeps (Figure 39). Sphagnum spp. form a continuous ground cover under a Carex spp. overstory. This is the only location of Drosera rotundifolia from the southern Rocky Mountains (Keammerer unpub. 1979). This Drosera also is known from Montana (Dorn 1984), and Drosera anglica is known from both Montana and Wyoming. Keammerer described five community types within the Keystone Bog. These are the Pinus contorta forest with dry understory, Pinus contorta

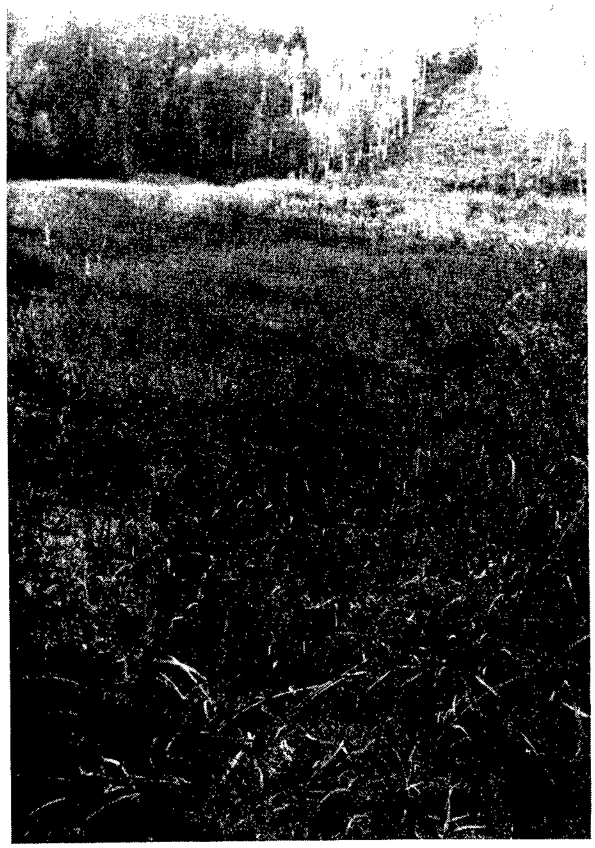


Figure 39. Keystone Bog, near Crested Butte, Colorado. Sphagnum spp. form a continuous carpet under the Carex spp. overstory. (Photo by D. J. Cooper.)

forest with wet understory, Carex aquatilis meadow, Carex utriculata meadow, and Eriophorum angustifolium-sedge meadow, which contains Drosera rotundifolia. Stand data for this community is presented in Table 22. Analyses of water samples from this community indicate a pH average of 4.29 for 36 plots, each sampled four times from July 29, 1980 to October 13, 1981. The pH ranged from 3.4 to 5.6. According to Sjors (1950) (Figure 33), peatlands with pH from 3.6 to 4.2 would be classified as bogs or extremely poor fens, and stands with pH of 4.29 and above would most likely be fens.

Table 22. Stand data for a Eriophorum angustifolium sedge community based on 15, 1-decimeter² plots. (From Keammerer 1979 unpubl.)

Species	Percent mean cover	Range of cover (%)	Frequency (%)
Eriophorum angustifolium	10.3	3-30	100
Carex aquatilis	6.5	0-31	66.7
Carex canescens	6.5	0-21	46.7
Deschampsia caespitosa	5.2	0-36	46.7
Vaccinium caespitosum	2.4	0-20	46.7
Betula glandulosa	1.5	0-15	20.0
Drosera rotundifolia	0.9	0-5	33.3
Eleocharis pauciflora	0.5	0-7	20.0
Calamagrostis scopulorum	0.1	0-2	6.7
Pinus contorta	0.4	0-1	53.3
Sphagnum spp.	61.5	0-100	0
Other moss spp.	4.5	0-34	0

One stand in Reeds Meadow at 3,080 m (10,100 ft) elevation in Colorado's Cross Creek Valley was fed by a side stream that drained nearly barren metamorphic rocks (Cooper 1986). This stand is dominated by Sphagnum warnstorfii, Tomenthypnum nitens, Aulacomnium palustre, Drepanocladus aduncus, and Calliergon stramineum that form hummocks upon which Betula glandulosa grows. The flora consists of many taxa not found elsewhere in Cross Creek fens, including Carex magellanica, C. lachenalii, and Sphagnum warnstorfii. This stand is separated from the main channel of Cross Creek by forest vegetation and appears not to receive overbank deposits of silts and is protected from high-energy, eroding stream flows. The surface of this stand is fed primarily by rainwater and stream water with very low electrical conductivity. It is obviously closely related to true bogs.

c. Marshes and meadows. Marsh and wet meadow communities occur on mineral soils and are dominated by herbaceous plant species. They can occur on the edge of fens; they have a higher summer soil temperature (Ramaley and

Robbins 1909) and greater soil aeration than fens, due to the reduced water-logging. Rapid oxidation of organic matter prevents the accumulation of peat. In colloquial use, marshes are generally wetter than meadows and, in many uses, include emergent and fen communities. Because there appears to be a continuum between marshes and wet meadows, they are lumped here until sufficient data and understanding are developed from the Rocky Mountain stands to separate them. Marshes may develop around deltas at lake inlets and on floodplains where overbank deposition of silts occurs. Marshes are usually associated with a permanent water source, have a water table close to the surface, and have water present for one or more months during the growing season (Tansley 1939). Four variables--siltation rate, aeration, temperature, and soil salinity--are important for determining the type of marsh community that can occur. Many of the same species that form fens can also form marshes. Thus, communities of <u>Carex</u> <u>utriculata</u>, <u>C</u>. <u>aquatilis</u>, and other species can be found also on mineral soil. Meadows occur in seasonally flooded basins and on flats; their soils are usually not wet during the entire growing season. Many meadows occur in, or below, late-lying snowbeds and have a water source for a few weeks during the growing season while the snow melts (Figures 40, 41, and 42) (Dix and Smiens 1967). These late-lying snowbeds are abundant throughout the Rocky Mountains, especially near upper treelimit, where snow blown down from alpine ridges accumulates in deep drifts (Ferchau 1969).

In the Subalpine Zone of Utah's Wasatch Plateau, valley bottoms and wetland soils are deep and contain higher organic matter than other soils in that area, but Ellison (1954) did not consider them to be organic soils. These uplands had been heavily overgrazed by livestock, which caused erosion on a large scale. As a result, lowland marsh soils are largely a product of soil deposition from higher ground, and not the product of peat accumulation. Marshes and meadows may be dominated by sedges, rushes, herbaceous dicots, and

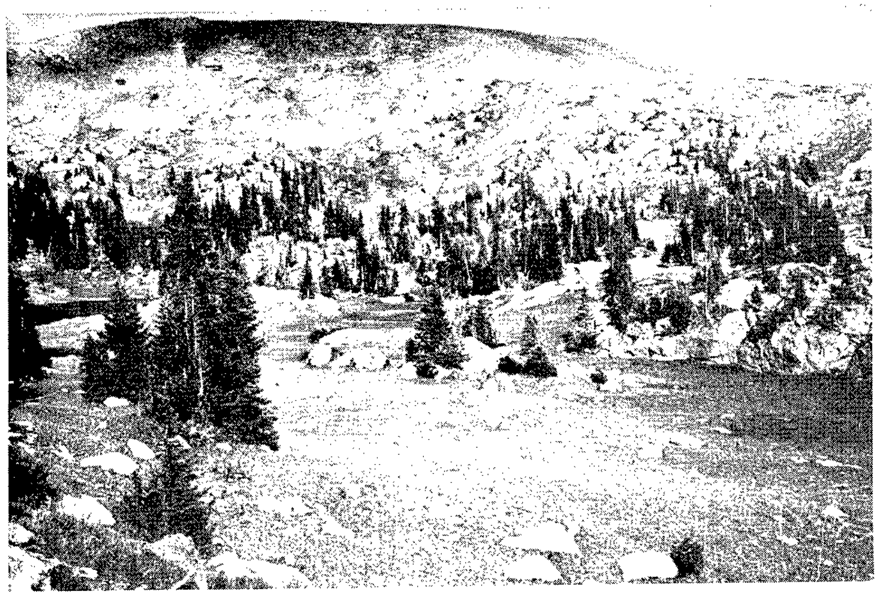


Figure 40. Meadows near treelimit created by deep snow accumulation at 3,477 m (11,400 ft) elevation in 10 Lakes Park, Rocky Mountain National Park, Colorado. (Photo by B. E. Willard.)

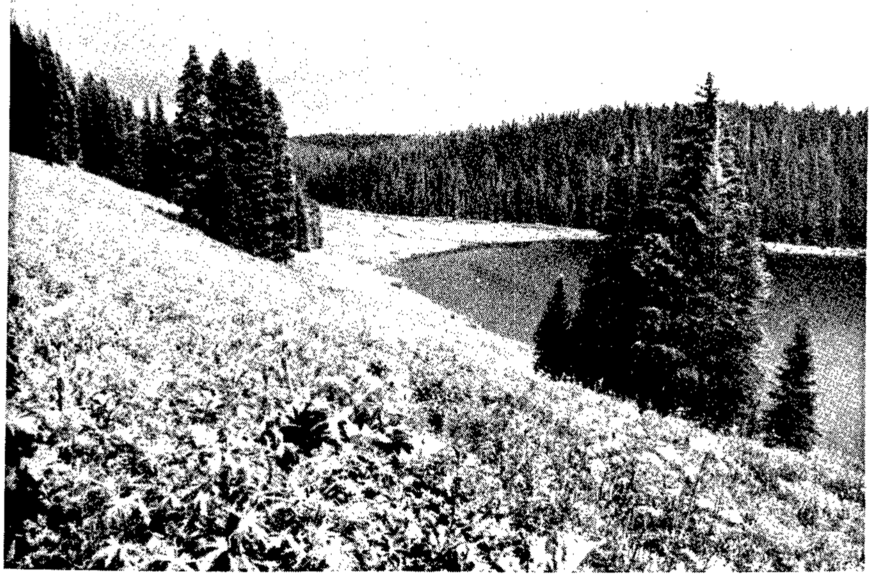


Figure 41. Meadows on steep hillsides and around lakes are created by late-lying snow melt and by seeps on Grand Mesa, Colorado at 3,050 m (10,000 ft) elevation. The dominant herbaceous species shown include *Delphinium barbeyi*, *Aconitum columbianum*, *Heracleum sphondylium*, *Corydalis caseana*, *Angelica grayi*, and *Mertensia ciliata*. (Photo by D. J. Cooper.)

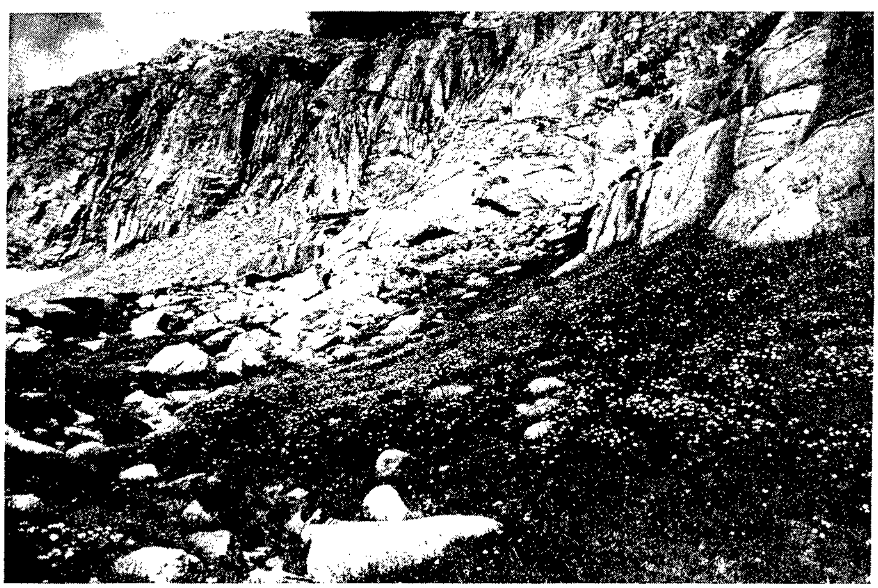


Figure 42. Meadow in late-lying snowbed is dominated by *Erigeron peregrinus*, near Crystal Lake, Rocky Mountain National Park, Colorado, at 3,447 m (11,300 ft) elevation. (Photo by B. E. Willard.)

other groups of species and have either a saline or fresh water source. Most irrigated wetlands in the Rocky Mountains would be classified as marshes or meadows, since they occur on mineral soils and are dominated by herbaceous species.

c.1. Marshes and meadows with fresh water. Seasonally saturated, but summer dry, mesic meadows occur at the drier end of the wetland soil moisture gradient in Big Meadows at 2,867 m (9,400 ft) elevation in Rocky Mountain National Park (Bierly 1972). The relationship of this mesic grass meadow with regard to autumn water table and thickness of peat can be seen in Figure 43. Deschampsia caespitosa, Danthonia intermedia, and Juncus drummondii (Editor's note: This may be J. parryi, which is very similar and grows at a lower elevation, whereas J. drummondii is found mainly above treelimit.) are the dominant species. Subordinate species include Viola adunca, Penstemon whippleanus, Carex siccata, C. arapahoensis, Erigeron peregrinus, Koeleria macrantha, and Agoseris glauca. No mosses occur in this community, and soils are the most nutrient-rich found in the Big Meadows area. This is due both to slope wash bringing nutrients from adjacent forest stands and rapid recycling of litter.

On recent alluvial sand in Big Meadows, communities dominated by Deschampsia caespitosa, Calamagrostis canadensis, Festuca ovina, and Carex aquatilis occur. These communities are moderately well-drained and have a deep water table at the end of the growing season. Less abundant species include Polemonium occidentalis, Arabis drummondii, Galium boreale, and Potentilla rupicola.

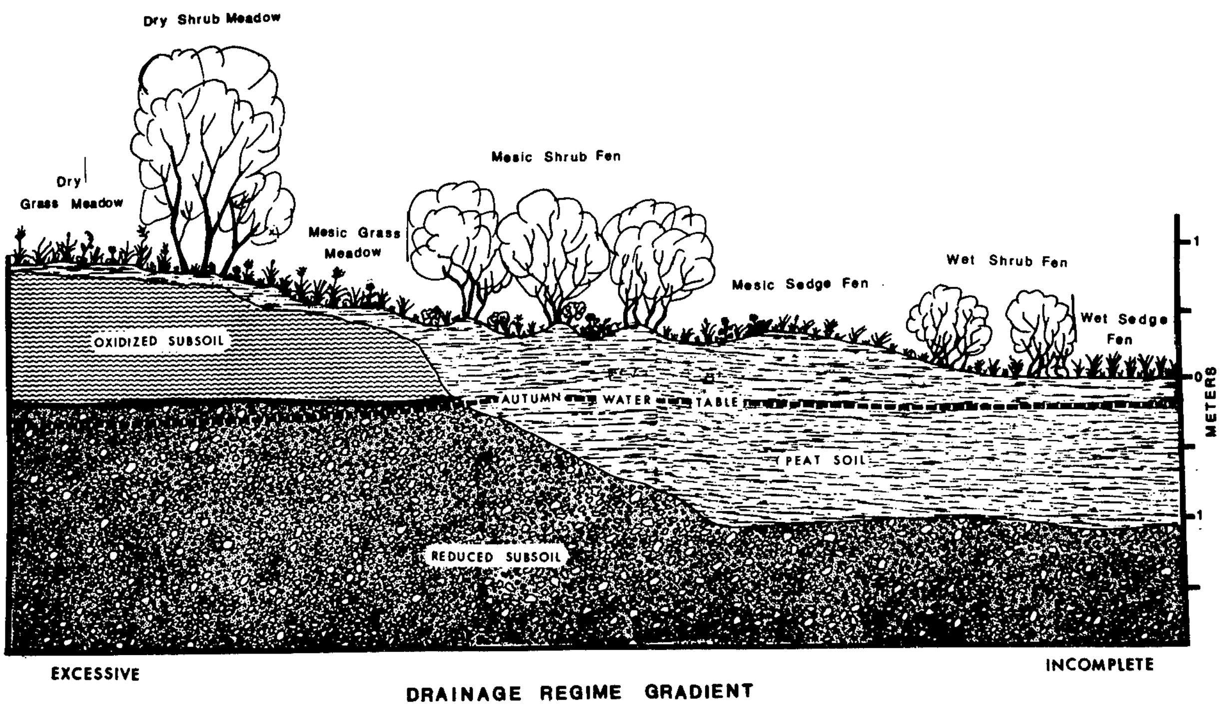


Figure 43. Drainage regime gradient in Big Meadows, Rocky Mountain National Park, Colorado, at 2,867 m (9,400 ft) elevation. (From Bierly 1972.)

In Utah's Wasatch Plateau, communities dominated by Cardamine cordifolia, Caltha leptosepala, Pedicularis groenlandica, Juncus balticus, Carex festivella, Eleocharis pauciflora, and Phleum alpinum have been reduced in abundance where overgrazing by sheep has caused soil erosion and gullying (Ellison 1954). The gullying caused a depression of the water table.

Ribbon forests are interesting features created by the interaction of wind, snow, and vegetation in areas with regionally or locally heavy snow accumulations (Billings 1969; Buckner 1977), such as in Wyoming's Medicine Bow Mountains and Colorado's Front and Park Ranges. Ribbon forests form and are maintained by wind striking the forest edge, eddying to the lee of these trees, and depositing snow where it eddies. Along the edge of ribbon forests, the accumulation of snow may be too deep for tree seedings to survive, and snow glades develop, which may be wet enough to sustain wetland species, and communities develop dominated by Deschampsia caespitosa, Sibbaldia procumbens, and Juncus drummondii. Other common taxa may include Erythronium grandiflorum, Erigeron melanocephalus, and Erigeron peregrinus.

In west- and south-central Colorado from about 3,203 m (10,500 ft) elevation to treelimit, mesic meadow communities characterized by Corydalis caseana are found.

Communities dominated by Veratrum tenuipetalum occur in the wettest parts of mesic meadows above Grand Lake, Colorado (Johnson 1941). Similar wetland communities are common throughout the Rocky Mountains, and Veratrum may indicate overgrazing (Weber 1976). In western Montana, similar communities are characterized by Veratrum viride.

Carex nigricans dominates snowpatches in the Subalpine Zone in north-central Colorado (Ramaley 1919). Carex illota or C. ebenea dominates mesic subalpine marsh communities in Wyoming's Medicine Bow Mountains (Starr 1974), and C. illota or Carex vernacula also form communities on lake shores, near springs, and below snowpatches in Colorado's Front Range (Komarkova 1979). Carex festivella dominates Stage 6 in glacial lake succession in Boulder Park, Colorado (Robbins 1918). In Rio Blanco County in western Colorado, Poa agassizensis dominates wet meadow communities with Carex praegracilis, C. nebraskensis, and Juncus arcticus (WRD, Northern Coal 1980a). Numerous other marsh and wet meadow types likely exist but have not yet been described in the Rocky Mountains. Glyceria borealis is abundant in many irrigated wetlands in Colorado's intermountain San Luis Valley and in the Big Hole National Battlefield, Montana (Pierce 1982).

Wet meadows and marshes that are irrigated by man for agricultural reasons are abundant in the mountain parks and intermountain basins. The vegetation of these wetlands, which have primarily mineral soils, is marshes and meadows (Figure 44).

Figure 44. Irrigated meadows along the Gunnison River, near Gunnison, Colorado, at 2,349 m, (7,700 ft) elevation. (Photo by D. J. Cooper.)

c.2. Marshes and meadows with saline water. Almost all rocks liberate considerable quantities of soluble salts as they weather (Daubenmire 1974). In regions of high rainfall, these salts are leached into streams and carried away from the area. Where evaporation exceeds precipitation, there is so little movement of water through the soil that salts formed by rock weathering, or blown in by wind, remain in high concentration in the soil. While accumulation of salts is not a factor throughout much of the Rocky Mountain area, it is a critical limiting factor in many of the intermountain basins, such as Colorado's San Luis Valley, Wyoming's Big Horn Basin, and the intermountain basins of southwestern Montana, where annual precipitation is quite low and large, relatively flat areas with fine-textured soils underlain by hundreds of meters of alluvial sediment may perch the water table. Where the water table is close to the surface, evaporation from the surface horizons during dry weather lifts salts to the soil surface and leaves a salt crust as the water enters the air. During rainy weather, these salts are transported downward.

Plants inhabiting alkaline soils must be able to tolerate high concentrations of salts and periods of drought. Sodium in soils at concentrations of 15% or greater of the adsorbed cations is injurious to glykophytes (sweet plants) (Daubenmire 1974). Because salts interfere with absorption of water by glykophytes, saline soils have long been considered "physiologically dry" for glykophytes, although physically, these soils may be wet.

There are few plant species that can proliferate on alkali soils, yet Sarcobatus vermiculatus, Distichlis spicata var. stricta, Sporobolus airoides,

Puccinellia airoides and other species are all common. These species are halophytes and can easily absorb water with high concentrations of certain ions, most notably sodium (Oosting 1956). Germination is inhibited by high salt concentrations and most halophytes germinate during the wet season when salts are partially leached downward into soils (Daubenmire 1974). These species are shallow-rooted to maximize the portion of the growing season when their roots are in soils with a lower salt concentration. Because the soils in saline and alkaline Rocky Mountain wetlands are usually waterlogged for portions of each year, shallow-rooting is equally important for aeration of roots. Many halophytes excrete superfluous salt by means of special glands, e.g., Distichlis, while others, such as Tamarix pentandra, secrete salts directly through the cuticle. Primary productivity in saline marshes is usually low, and shrubs are usually widely spaced, but grasses such as Distichlis may form a turf (Figure 45).

Figure 45. Turf of Distichlis spicata var. stricta and clumps of Sporobolus airoides on seasonally wet alkaline soil, San Luis Valley, Colorado, at about 2,593 m (8,500 ft) elevation. (Photo by D. J. Cooper.)

Perhaps the most widespread saline marsh or meadow type is dominated by Distichlis, which occurs widely throughout the Rocky Mountain region in both wet and relatively dry soils. Communities dominated by Distichlis occur on soils with better drainage than other saline wetland communities dominated by Triglochin maritimum, Puccinellia nuttalliana, and Salicornia rubra in Colorado's South Park (Ungar 1974). Comparison of soil characteristics and floristic composition for five community types dominated by these four species are shown in Table 23.

Table 23. Soil moisture, pH, and salinity characteristics in plant communities in South Park, Colorado. (From Ungar 1974.)

	Community				
	Ds[a]	Tm[b]	wTm[c]	Pn[d]	Sr[e]
Number of samples	15	10	5	5	20
Soil moisture (%)	13.9	32.7	212.3	59.1	38.9
Conductivity (µmhos/cm)	45.6	34.0	26.0	11.0	44.0
Total salts (%)	2.9	2.1	1.6	0.8	2.8
pH median	7.7	8.1	8.1	8.1	7.6
Species	Relative crown cover (%) in each community				
Distichlis stricta	93	+[f]	0	0	0
Trighlochin maritima	4	82	58	7	+
Puccinellia nuttalliana	+	11	22	64	1
Salicornia rubra	3	5	2	28	78
Ranunculus cymbalaria	0	1	14	0	0
Suaeda depressa	+	0	0	0	21
Scirpus americanus	0	+	3	0	0
Aster brachyactis	0	+	+	0	0
Aster pauciflorus	0	+	+	0	0
Juncus bufonius	0	0	+	0	0

[a]Ds = *Distichlis stricta*

[b]Tm = *Triglochin maritimum*

[c]wTm = wet *Triglochin maritimum*

[d]Pn = *Puccinellia nuttalliana*

[e]Sr = *Salicornia rubra*

[f]+ = presence, <1.

Ten soil samples in Distichlis communities taken by Ungar (1974) contained an average total of 3.6% salt. Broken down by ionic content, samples contained an average of 2.3% chloride, 0.6% sodium, 0.2% potassium, 0.3% calcium, and 0.1% magnesium per sample. The ionic composition of salts in the Triglochin maritimum and Salicornia rubra communities were very similar. Salicornia rubra is an invader of highly saline salt flat soils. There is very low floristic diversity on these sites due to high osmotic stress, which eliminates all but the most salt-tolerant species. Seedlings are established in protected sites, cracks in the clay soil caused by expansion and contraction, which provide safe sites for ecesis. Ungar noted that the salt flats in Colorado were more similar to the salt flats in South Dakota, Saskatchewan, and Utah than to those found in Oklahoma, Kansas, and Nebraska.

From Colorado's San Luis Valley, Ramaley (1942) described an inner meadow zone around lakes, dominated by Distichlis, Equisetum arvense, Juncus balticus, and Hordeum jubatum. Around the San Luis Lakes in this same region, three bands of vegetation occur: the first is dominated by Eleocharis palustris, the second by Cleome sonorae, and the third by Distichlis, Sporobolus cryptandrus, Agropyron smithii, Juncus balticus, and Carex festivella. Communities dominated by any of these species, along with Triglochin maritimum (Figure 46), Muhlenbergia asperifolia, and Sporobolus airoides are found in the San Luis Valley and elsewhere in the arid parks and intermountain basins.

Figure 46. Meadow of Triglochin maritimum on seasonally wet alkaline soil, San Luis Valley, Colorado, at about 2,562 m (8,400 ft) elevation. (Photo by D. J. Cooper.)

Numerous reports of Distichlis communities exist, and many are wetlands. In western Utah, and around the Great Salt Lake, Distichlis is abundant as a grassland community with Allenrolfea occidentalis, Salicornia utahensis, Sporobolus airoides, S. cryptandrus, Puccinellia nuttalliana, Triglochin maritimum, and Juncus balticus (Flowers 1934; Nelson 1955; Bolen 1964). This vegetation forms a number of communities similar to those described by Ungar (1974) for Colorado parks. In New Mexico, Distichlis occurs with Allenrolfea and Suaeda spp. (Dick-Peddie 1985). On strands around the Great Salt Lake, the following five zones occur, hypothetically in some seral order: (1) Salicornia rubra - S. utahensis - Allenrolfea occidentalis; (2) Suaeda erecta; (3) Distichlis stricta; (4) Suaeada spp.; and (5) Atriplex spp., Sarcobatus vermiculatus, Chrysothamnus nauseosus, and other spp. (Flowers 1934).

On exposed shores around ponds on saline soil in Alberta, Canada, the following species are the most abundant: Salicornia rubra, Distichlis stricta, Suaeda erecta, Atriplex hastata, Triglochin maritimum, Puccinellia nuttalliana, Suaeda depressa, Spergularia salina, Plantago eriopoda, and Glaux maritimum. These are almost exactly the same dominants as Ungar (1974) and other investigators report for most regions of western and central North America. Because the chief factor controlling species distribution is tolerance to salinity stress, local environmental differences, such as temperature and length of growing season, seem to be less important in determining floristic composition of stands, and the few species adapted for high water table and high salinity stress are widespread and abundant.

Shrub-dominated wetlands. Shrubs may dominate several different types of ecological situations in wetlands of the Rocky Mountains. On minerotrophic organic soils, carrs occur. On ombrotrophic organic soils, shrub-dominated bogs occur. On mineral soils with saline or fresh water sources, shrub wetlands occur.

There are several ecological differences between fens and dense carrs, as well as between marshes and shrub wetlands. For example, fens occur in the wettest portion of the moisture gradient, whereas carrs may occupy more mesic soils with greater aeration and better drainage (Figures 43 and 47). Shrubs reduce light reaching the ground surface and their leaf litter provides a rich humus. Tall herbaceous species, such as Polemonium caeruleum, and mosses, such as Hypnum spp., that can tolerate the shading, occur only under the shrubs, making each shrub and the plants under its canopy a small island of floristic diversity. By contrast, each type of sedge fen is floristically homogeneous throughout, therefore monotonous. Sedge fens and carrs do appear to grade into each other in places. According to Phillips (1977), fens with 25% or greater coverage by shrubs are carrs. Hallock (1985) reports that in the Colorado Front Range, montane shrub wetlands at 2,440 to 2,745 m (8,000 - 9,000 ft) have mineral soils, and subalpine carrs at 2,745 to 3,355 m (9,000 - 11,000 ft) have peaty soils.

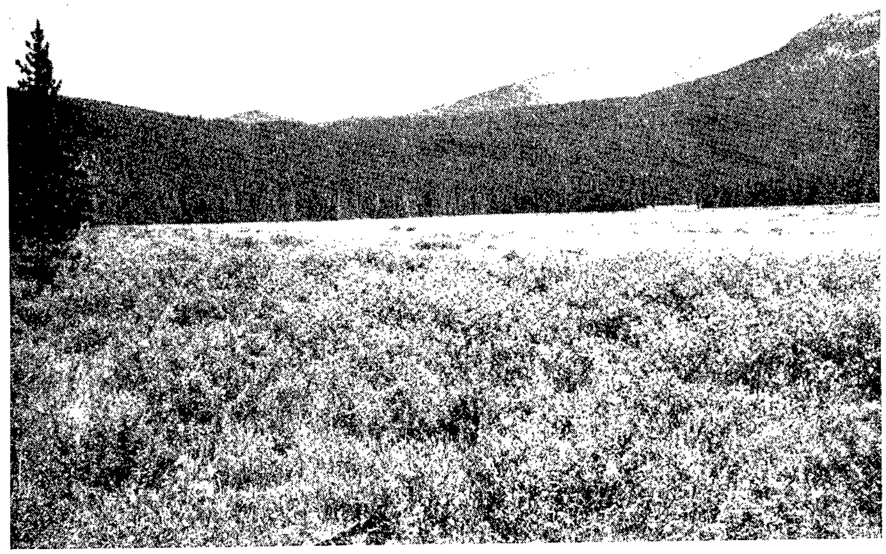


Figure 47. Shrub-dominated wetlands occur in more well-drained habitats on the edges of sedge fens in Big Meadows, Rocky Mountain National Park, Colorado, at 2,867 m (9,400 ft) elevation. (Photo by B. E. Willard.)

Montane shrub wetlands have a density of 640 breeding birds per 40 ha (100 ac), Subalpine carrs have 256 birds per 40 ha, and Alpine carrs have 107 birds per 40 ha (Hallock 1985). The Montane shrub wetlands avifauna consists of 21 bird species, primarily Wilson's warbler (Wilsonia pusilla), Lincoln's sparrow (Melospiza lincolnii), song sparrow (M. melodia), American robin (Turdus migratorius), dusky flycatcher (Empidonax obserholseri), and others. Song sparrow, yellow warbler (Dendrocia petechia), and blackheaded grosbeak (Pheucticus melanocephalus) reach their maximum elevation in the Montane Zone. Subalpine carrs have an avifauna composed primarily of Wilson's warbler, Lincoln's sparrow, and white-crowned sparrow (Zonotrichia leacophrys).

Abundance of Salix spp. is the most important factor determining which areas are used by white-tailed ptarmigan (Lagopus leucurus) in winter, and where breeding territories are established in spring (Braun 1969; May 1970; Hoffman 1974). White-tailed ptarmigan depend upon Salix spp. for 92% of their winter, 67% of their spring, and 44% of their fall food (May 1970). These willows may occur near treelimit or lower in the Upper Subalpine Zone, in open

or dense shrublands, in carrs, and along stream courses. The most important forages for moose (Alces americana) introduced into vacant range in Colorado's North Park (Nowlin 1985) are Salix planifolia, S. pseudocordata, S. drummondiana, and S. monticola, which indicates further the importance of shrub wetland habitats for supporting wildlife.

a. Carrs. Carrs occur on minerotropic peat; they may have either a very dense vegetative cover with shrubs forming thickets, or the overstory may be open and scattered, but usually there is abundant water, which retards decomposition of peat (Figure 48).

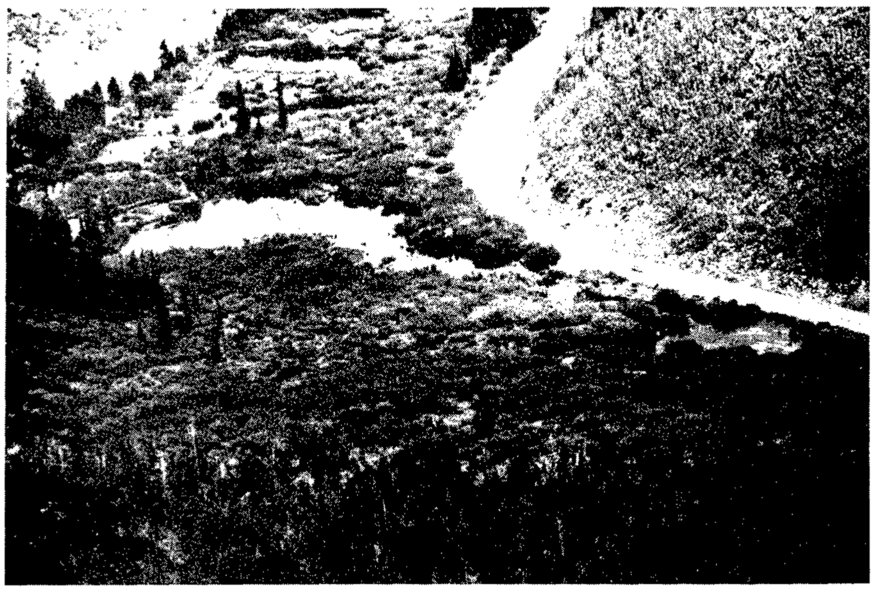


Figure 48. Permanently wet carr in Hidden Valley, Rocky Mountain National Park, Colorado, at 2,791 m (9,150 ft) elevation. Beaver dams help keep this area flooded and a large lateral moraine restricts drainage from the valley. (Photo by B. E. Willard.)

In Colorado's Laramie River Valley, Phillips (1977) described four shrub-dominated communities, two of which occur on organic soils and two on mineral soils (Figure 49). Bierly (1972) also described two carr types from Big Meadows, Rocky Mountain National Park (he refers to them as "wet shrub fen" and "mesic shrub fen"). On wet, highly humified soils in the Laramie Valley, Salix planifolia (S. phylicifolia ssp. planifolia) is the dominant species (Table 24), whereas on wet, low humified peat Salix planifolia, Betula glandulosa, and Salix wolfii are codominants. Salix candida occurs there, one of two known locations in Colorado, and Menyanthes trifoliata, a rare species in Colorado, also occurs.

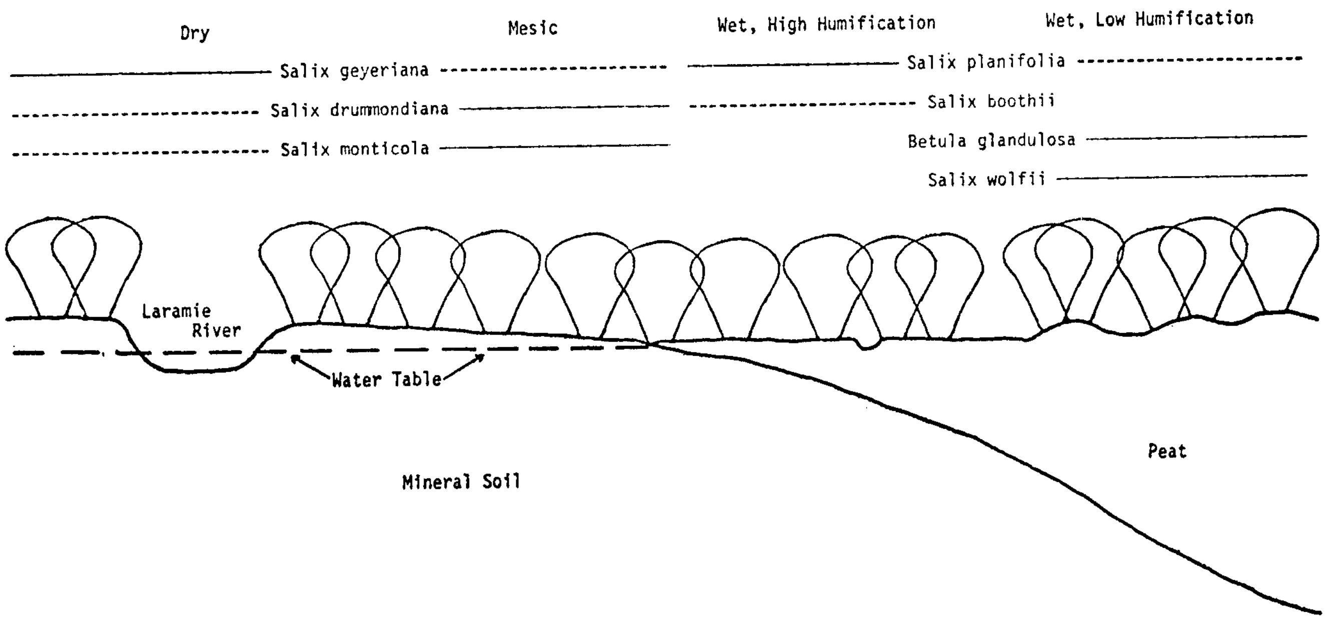


Figure 49. Diagram comparing the landscape position of four shrub-dominated communities in the Laramie River Valley, Colorado. (From Phillips 1977.) The wet, low humification and wet, high humification types on deep peat are carrs in the present classification, while the dry and mesic shrub types are classified as shrub wetlands on mineral soil with a fresh water source.

Hess (1981) reports three community types (Hess calls them habitat types) dominated by Salix planifolia; one occurs in the Alpine Zone (Salix planifolia - Carex scopulorum); one occurs on mineral soil in the Subalpine Zone (Salix planifolia - Deschampsia caespitosa); and one is a carr (Salix planifolia - Carex aquatilis). The third type occurs in a more hydric environment than any other shrub type in the Montane or Subalpine of the Roosevelt and Arapahoe National Forests of Colorado between 2,725 and 3,300 m (8,940 - 10,827 ft) elevation (Table 24). This carr type occurs on topographically low terrain of valley bottoms, landscape depressions, and in forest openings inundated with spring snowmelt. The water table is near the surface throughout the growing season, thus allowing organic soils to develop. Soils are classified as Typic Cryohemist on poorly-drained sites and Typic Cryosaprists on sites with improved drainage. Soils are peaty muck to mucky peat and are greater than 1 m (3.3 ft), with pH of the organic matter ranging from 5.0 to 6.6.

Table 24. Stand data for carrs dominated by Salix planifolia.

Species	Percent coverage (constancy) Hess (1981)[a]	Phillips (1977)[b] Low	Phillips (1977)[b] High
Salix planifolia	52 (100)	20	39
Betula glandulosa	10 (100)	23	6
Salix wolfii	1 (50)	19	0
Calamagrostis canadensis	2 (75)	8	5
Carex aquatilis	53 (100)	85	72
Carex utriculata	14 (100)	58	63
Deschampsia caespitosa	1 (75)	0	0
Eleocharis pauciflora	1 (100)	0	0
Caltha leptosepala	4 (100)	0	0
Sedum rhodanthum (Clementsia rhodantha)	3 (75)	0	0
Erigeron peregrinus	1 (75)	0	0
Pedicularis groenlandicum	1 (100)	55	22
Salix boothii	0	6	13
Salix drummondiana	0	1	1
Salix monticola	0	2	4
Salix geyeriana	0	6	9
Eleocharis rostellata	0	27	11
Polemonium caeruleum	0	65	29
Dodecatheon puluchellum	0	12	22
Carum carvi	0	13	38
Equisetum arvense	0	6	50
Viola palustris	0	12	18
Castilleja sepentrionalis	0	12	13
Poa palustris	0	7	18
Pyrola asarifolia	0	10	8
Fragaria vesca	0	11	11
Mertensia ciliata	0	3	4
Geranium richardsonii	0	6	8
Phleum alpinum	0	5	5
Geum macrophyllum	0	6	4

[a]Hess' (1981) data are from four stands of his Salix planifolia-Carex aquatilis habitat type.

[b]Phillips' (1977) data are for his wet, low humification carr, and wet, high humification carr.

Salix planifolia dominates subalpine willow thickets below 3,538 m (11,600 ft) elevation at Summitville, in Colorado's San Juan Mountains (Keammerer and Keammerer 1983), along with Salix brachycarpa, Caltha leptosepala, Ligularia pudica, and L. amplectens. Salix planifolia dominates riparian communities in Colorado's North Park (Knopf and Cannon 1982) and decreases in abundance with increasing distance from streams (Cannon and Knopf 1982), which indicates it is growing on the wettest sites. It occurs in North Park with Salix pseudocordata, S. monticola, S. drummondiana, S. geyeriana, and S. caudata. Salix planifolia occurs where there is shallow snow, along streams, and in shallow basins produced by solifluction. Salix planifolia is replaced by Carex aquatilis where the soil is too wet and by Deschampsia caespitosa where the snow persists for too long (Heifner 1974).

Communities dominated by Salix brachycarpa, S. wolfii, and Betula glandulosa occur in Rocky Mountain National Park's Big Meadows (Bierly 1972) on shallow peaty soils. These soils have high base saturation due to an influx of mineral material from adjacent forest stands, and a water table depth of 86 cm (33.9 in) in late summer. Calamagrostis canadensis, Deschampsia caespitosa, Carex aquatilis, and Festuca ovina are also common species. Salix brachycarpa also dominates on moderately deep 53 cm (20.9 in) peat, where the water table averages 30 cm (11.8 in) in late summer, cation exchange capacity is high, and bulk density of soils is low. Carex aquatilis, C. utriculata, C. canescens, Caltha leptosepala, Sedum rhodanthum, Pedicularis groenlandicum, Pohlia nutans, Polytrichum juniperinum, Mnium spp., and Calliergon cuspidatum were most abundant.

In western Wyoming, the Salix wolfii - Swertia perennis community type (Table 25) occurs where soils are slow to dry, are Aquic Cryofluvents with water table at 80 cm (31.5 in), or are Terric Borofibrists with water table at 8 cm (3.5 in). The ground surface is mossy, resilient, and hummocky with shrubs occurring on the hummocks. Productivity averages 141.4 g/m^2 and ranges from 127 to 155 g/m^2. Of this productivity, 105 g are grasses and sedges, and 33 g are shrubs. Salix wolfii also dominates a willow phase, along with Betula glandulosa, Pentaphylloides floribunda, and Salix drummondiana in Yeoman Park, Sawatch Mountains, Colorado (WRD, for Adams Rib 1983).

Carrs in the Pine Butte Fen, Montana (Lesica 1982), are dominated by Betula glandulosa, Salix candida, Salix planifolia, Carex simulata, Campylium stellatum, and Carex utriculata - C. aquatilis (Table 26). This wetland is along the eastern Rocky Mountain front and is a mosaic of carrs and fens. It is underlain by glacial outwash composed of calcareous shales and limestones. Soils are mucky peat where hummock and hollow topography occurs. Moving water through these carrs provides better oxygen and nutrients than peatlands with impermeable peat that the water flows around. Carrs are associated with soils having better oxygen and nutrient relations than sites occupied by fens.

Table 25. Stand data for a Salix wolfii-Swertia perennis community. (From Matz and Graham 1982.) Constancy on 10-point scale.

Species	Percent coverage (constancy) Mutz and Graham (1982)
Salix wolfii	16 (10)
Betula glandulosa	10 (10)
Carex simulata	78 (10)
Juncus balticus (J. arcticus)	18 (5)
Ledum groenlandicum	1 (10)
Swertia perennis	4 (10)[a]
Deschampsia caespitosa	+ (10)
Equisetum laevigatum	+ (5)
Polemonium occidentalis	+ (5)

[a]+ = presence, <1.

Table 26. Carrs in Pine Butte Fen, Montana. (Data from Lesica 1982.) Species values are prominence values calculated by dividing absolute frequency by percent canopy cover.

Stand number	3	7	6	10
Water cover (%)	0	0	0	45
Bare ground (%)	0	0	0	0
Shrub height dm	13	18	12	18
Conductivity (μmho/cm)	560	395	520	510
pH	6.7	6.8	6.6	6.9
Species	Prominence values by stand number			
Betula glandulosa	137	41	76	190
Cornus stolonifera	0	18	24	12
Pentaphylloides floribunda	118	1	22	0
Salix candida	1	1	74	2
Salix planifolia	1	11	1	75
Equisetum arvense	0	32	0	0
Equisetum laevigatum	1	38	1	7
Triglochin maritimum	9	6	23	0
Galium boreale	23	6	15	0
Carex lasiocarpa	32	17	0	0
Carex utriculata-C. aquatilis	170	0	0	311
Carex aquatilis	0	165	0	0
Carex buxbaumii	170	0	1	0
Carex simulata	0	2	233	0
Drepanocladus revolvens	25	0	3	0
Campylium stellatum	158	71	207	1
Rhynchostegiella compacta	29	54	89	1
Calliergon giganteum	0	46	0	0

b. Shrub-dominated bogs. Shrub wetlands with soils of low humification in Colorado's Laramie River Valley, described by Phillips (1977) (Table 24), have an abundance of *Betula glandulosa* with *Salix wolfii* and *S. planifolia*. There is little water flushing from or across this type, and it is the most ombrotrophic community occurring in the Laramie River Valley. Whether or not this community is a true bog is not known.

c. Shrub-dominated wetlands with mineral soils and fresh water. Many species that dominate carrs in the Rocky Mountains can also dominate communities on mineral soils. For example, in Colorado's Cross Creek Valley, *Salix planifolia* dominates shrublands on soils that are primarily silt from overbank deposition (Table 27 and Figure 50). These stands occur along Cross Creek on soils with water table at 70 to 100 cm (27.6 - 39.4 in), and most roots occur in the top 15 cm (5.9 in) (Cooper 1986). A layer of organic matter occurs at the soil surface, but little is seen in the soil profile. The *Salix planifolia* - *Deschampsia caespitosa* habitat (community) type (Table 27) of Hess (1981) is common from 2,850 to 3,400 m (9,351 - 11,155 ft) elevation in forest openings and valley bottoms with high winter snow accumulation. Soils are moist during the entire growing season and are well drained. Soils are primarily mineral, classified as Aquic Cryumbrepts, with a pH of 5.2 to 6.0, and are 17 to 44 cm (6.7 - 17.3 in) in depth.

In western Wyoming, *Salix wolfii* can dominate mineral soils as well as the organic soils of carrs described in the last section (Mutz and Graham 1982). In Rocky Mountain National Park's Big Meadows, *Salix wolfii*, *Pentaphylloides floribunda*, and *Betula glandulosa* dominate the "dry shrub meadows." This community occurs on alluvial ridges, where there is some soil profile development and the water table is below the root zone in midsummer. Few sun-loving forbs occur in this community, but a large number of shade-tolerant species do, such as *Stellaria longipes*, *Thalictrum alpinum*, *Festuca ovina* (*F. brachyphylla*, authors), and the mosses *Aulacomnium palustre* and *Polytrichum commune* (Bierly 1972).

In Colorado's Laramie River Valley, two shrub wetland communities occur on mineral soil. *Salix geyeriana*, *S. drummondiana*, and *S. monticola* are dominants of a mesic community on loamy soils that is characterized by an abundance of *Carex utriculata* and *C. aquatilis*, while *Poa pratensis*, *Achillea lanulosa*, and *Taraxacum officinale* characterize drier alluvial plains with sandy loam soils. The "dry" *Salix geyeriana* community is the most abundant shrub wetland community in the Laramie River Valley. The *Salix geyeriana* - *Calamagrostis canadensis* habitat (community) type (Table 28) is an important shrub wetland in most wet areas in the Montane Zone of the Arapahoe and Roosevelt National Forests of Colorado (Hess 1981). It occurs in valley bottoms adjacent to river terraces at 2,575 to 2,750 m (8,449 - 9,023 ft), where soils are saturated by spring floods and the ground water is well below the surface during the growing season. Soils are moderately well drained, primarily mineral, classified as Typic and Aquic Cryaquolls, 44 to 79 cm (17.3 - 31.1 in) deep, and have a pH of 6.0 to 6.8. The abundance of nonnative plant species indicates human impact, such as livestock grazing, making this community a zootic climax. Hess recognized that there was low similarity between the four stands he sampled and the possible need to distinguish phases.

Table 27. Stand data for shrub wetland communities dominated by *Salix planifolia* on mineral soil.

Species	Percent coverage (constancy) Hess (1981)[a]	Cooper (1985)[b]		
Salix planifolia	41 (100)	90	90	80
Salix wolfii	+[c] (25)	0	0	0
Deschampsia caespitosa	41 (100)	0	0	0
Carex aquatilis	4 (100)	5	10	0
Carex microptera	1 (50)	0	0	0
Eleocharis pauciflora	1 (75)	0	0	0
Phleum alpinum	1 (75)	0	0	0
Achillea lanulosa	1 (50)	0	0	0
Caltha leptosepala	19 (100)	0	0	0
Castilleja septentrionalis	1 (75)	0	0	0
Epilobium lactiflorum	1 (50)	0	0	0
Erigeron peregrinus	2 (100)	0	0	0
Ligusticum porteri	1 (50)	0	0	0
Pedicularis groenlandicum	2 (100)	0	0	0
Bistorta bistortoides	1 (50)	0	0	0
Potentilla diversifolia	1 (75)	0	0	0
Ranunculus alismaefolius	1 (50)	0	0	0
Sedum rhodanthum (*Clementsia rhodantha*)	2 (50)	0	0	0
Senecio crocatus	1 (75)	0	0	0
Veronica wormskjoldii	1 (100)	0	0	0
Mertensia ciliata	0	1	5	10
Aconitum columbianum	0	5	3	1
Thalictrum sparsiflorum	0	1	0	1
Cardamine cordifolia	0	2	0	0
Senecio triangularis	0	+	0	0
Climacium dendroides	0	15	0	25
Calamagrostis canadensis	0	0	5	20
Geum macrophyllum	0	0	5	1
Pentaphylloides floribunda	0	0	1	0
Betula glandulosa	0	0	0	10

[a]Hess' (1981) data are from four stands of the *Salix planifolia*-*Deschampsia caespitosa* habitat (community) type.

[b]Cooper's (1986) data are from stand numbers 85-52, 85-44, and 85-35.

[c]+ = presence, <1.

Figure 50. A complex pattern of river meanders, oxbows, and side streams, in Reeds Meadow, Cross Creek Valley, Sawatch Range, Colorado. Most of this area is dominated by *Salix planifolia*, which forms shrub wetlands and carrs in a few places. (Photo by D. J. Cooper.)

Pentaphylloides floribunda (*Potentilla fruticosa*) dominates wetland communities throughout the Rocky Mountains, but few data were found for these types. In western Wyoming, Mutz and Graham (1982) described the *Potentilla fruticosa* - *Deschampsia caespitosa* community type that occurs in valley bottoms, in many places as narrow bands along valley edges (Table 29). This community occurs on soils that are Typic, Aquic Calcic, and Cumulic Cryoborolls. *Potentilla fruticosa* communities are also reported by Pierce (1980) for floodplains of the Bighole National Battlefield in Wyoming and the *Potentilla fruticosa* - *Festuca idahoensis* habitat type from the Bighorn Mountains of Wyoming (Despain 1973). This species also forms circular zones around "willow marshes" on the White River plateau in Colorado (Miller 1964). The *Pentaphylloides floribunda* - *Dugaldia hoopsii* - *Valeriana edulis* community is described by Boyce (1977) from the South Fork of the White River Valley of Colorado (Table 29). It has a relatively high water table and occurs between stands dominated by *Salix* spp. and grasslands. Soil collected in one stand had the following characteristics:

Depth (cm)	(in)	pH	Organic matter (%)
10	(3.9)	6.0	9.6
30	(11.8)	6.4	7.0
50	(19.9)	6.2	5.9

Table 28. Stand data for shrub wetland communities dominated by *Salix geyeriana* and *S. monticola*.

Species	Percent coverage (constancy) Hess (1981)	Phillips (1977)[a]	
Salix geyeriana	27 (100)	28	38
Salix monticola	23 (100)	18	17
Salix drummondiana	7 (100)	14	12
Salix boothii	0	11	9
Salix planifolia	0	12	0
Ribes inerme	1 (50)	0	0
Calamagrostis canadensis	43 (100)	47	27
Carex aquatilis	6 (75)	14	0
Carex festivella	3 (100)	0	0
Carex utriculata	3 (100)	44	0
Carex scoparia	2 (75)	0	0
Deschampsia caespitosa	1 (75)	0	0
Juncus longistylis	1 (100)	0	0
Phleum pratense	4 (100)	9	16
Poa pratensis	2 (100)	12	53
Poa reflexa	2 (100)	0	0
Trisetum wolfii	1 (75)	0	0
Achillea lanulosa	2 (100)	11	51
Castilleja septentrionalis	4 (75)	8	4
Erigeron peregrinus	3 (50)	0	0
Fragaria ovalis	4 (100)	18	37
Polemonium occidentalis	3 (50)	24	0
Potentilla pulcherrima	+ (100)[b]	0	0
Taraxacum officinale	4 (100)	30	69
Trifolium repens	7 (100)	0	0
Vicia americana	1 (75)	8	38
Equisetum arvense	0	27	12
Pyrola asarifolia	0	12	3
Mertensia ciliata	0	24	20
Carex microptera	0	14	9
Geranium richardsonii	0	16	14
Geum macrophyllum	0	28	26
Carex pachystachya	0	4	24

[a]Phillips' data are percent coverage for two stands.

[b]+ = presence, <1.

Table 29. Stand data for shrub wetland communities dominated by Pentaphylloides floribunda (Potentilla fruticosa).

Species	Percent coverage (constancy) Mutz and Graham (1982)[a]	Percent coverage (constancy) Boyce (1977)[b]
Pentaphylloides floribunda	29/(10)	44.5
Salix wolfii	2/(2)	0
Salix boothii	+/(2)[c]	0
Carex douglasii	4/(3)	0
Carex microptera	4/(7)	0
Carex praegracilis	5/(10)	0
Deschampsia caespitosa	31/(10)	0
Festuca idahoensis	2/(3)	0
Juncus balticus	8/(7)	0
Poa pratensis	1/(8)	0
Stipa columbiana	2/(2)	0
Achillea lanulosa	10/(2)	2.4
Fragaria virginiana	10/(8)	18.4
Potentilla gracilis	7/(5)	17.4
Valeriana occidentalis	5/(4)	0
Valeriana edulis	0	9.4
Solidago multiradiata	0	8.8
Vicia americana	0	5.7
Dugaldia hoopesii	0	8.6
Taraxacum officinale	0	8.0
Agropyron trachycaulon	0	3.2
Thalictrum fendleri	0	3.1
Bromopsis inermis	0	6.6
Festuca thurberi	0	8.3

[a]Pentaphylloides floribunda-Deschampsia caespitosa community from Mutz and Graham (1982). Constancy is on a 10-point scale.

[b]Boyce's data (1977) are average cover from the Pentaphylloides-Dugaldia-Valeriana association.

[c]+ = presence, <1.

Shrub-dominated communities are abundant at high elevation where snow is late-lying in small basins (Figure 51) and on broad gently rolling upland terrain (Figure 52). Other shrub-dominated communities on mineral soils that have been reported are the following: (1) Salix pseudocordata near Crested Butte, Colorado (Langenheim 1962), with Salix melanopsis and S. irrorata; (2) Salix barclayi, with S. drummondiana and S. pseudolapponica, also near Crested Butte (Langenheim 1962); (3) Salix drummondiana "shrub-swamp" communities, with water at or near the water surface, near Jackson Hole, Wyoming (Reed 1952), with Salix geyeriana, S. boothii, S. wolfii, and, where extra flooding occurs, S. caudata, S. drummondii, S. mackenziana, and S. melanopsis occur and dominate the tall willow community, with Carex aquatilis and Geum macrophyllum, in Yeoman Park, Sawatch Range, Colorado (WRD, Adams Rib 1983); (4) the Rhododendron albiflorum community around lakes in Colorado's Park Range, and to the north in Wyoming and Montana; the Salix bebbiana-dominated community in Wyoming (Shute 1981), Utah (Dixon 1935), and Idaho (Schlatterer 1972).

Figure 51. Shrub wetlands on mineral soil can occur in most snow accumulation basins at high elevation, such as near the head of the North Inlet, Rocky Mountain National Park, 3,264 to 3,508 m (10,700 to 11,500 ft) elevation. (Photo by B. E. Willard.)

Figure 52. Shrub wetlands on mineral soil can occur in broad upland areas near treelimit, such as this one on Guanella Pass, Colorado, Front Range. This is an important wintering area for white-tailed ptarmigan. (Photo by D. J. Cooper.)

d. Shrub-dominated wetlands with mineral soils and saline water. Sarcobatus vermiculatus is adapted to areas with poor drainage and high concentrations of salt in the soil (Dixon 1971) and may dominate areas where the water table is near the ground surface and where there is high salt and alkali content (Dix 1974) (Figure 53). It dominates saline wetlands in mountain parks and intermountain basins of the Rocky Mountains and many other areas of the West. Seedlings of this species can grow in soil with salt content of up to 2.5% (Hanson 1929). The stands may be flooded in early summer and occur with Sporobolus airoides, Distichlis spicata, and Agropyron smithii (Hanson 1929), but it is not known whether the shrub community follows grass-dominated communities in succession.

Two habitat types dominated by Sarcobatus vermiculatus occur in western Montana (Mueggler and Stewart 1980). These are the S. vermiculatus - Agropyron smithii type along streams in low-precipitation areas with saline and alkaline soils, and the S. vermiculatus-Elymus cinereus type, which forms a narrow band along floodplains. This latter type is poorly drained and saline-alkaline. Other important species occurring in these communities are Atriplex nuttallii and Chrysothamnus viscidiflorus.

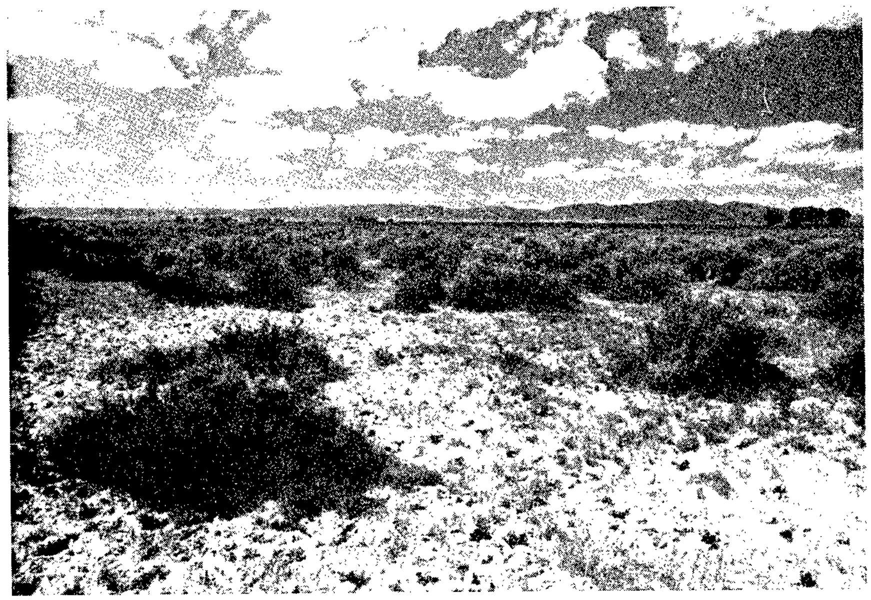


Figure 53. Shrub wetlands on mineral soil with a saline water source are dominated by Sacrobatus vermiculatus in intermountain basins and Western Slope river valleys of the Rocky Mountains, such as in Colorado's San Luis Valley. (Photo by D. J. Cooper.)

In New Mexico, the following habitat types occur: Sarcobatus vermiculatus - Chrysothamnus nauseosus var. graveolens, S. vermiculatus - Atriplex canescens, and S. vermiculatus -Suaeda suffrutescens - Distichlis stricta (Dick-Peddie 1985). In the wetter central portion of Colorado's San Luis Valley, the Sarcobatus vermiculatus - Chrysothamnus sp. association occurs (Enright 1971). It typically has an understory of Muhlenbergia asperifolia, Sporobolus spp., and, in areas of extreme alkalinity, Distichlis stricta. Sarcobatus replaces species of Chrysothamnus in areas of saline soil or high water table. Irrigation in the San Luis Valley has resulted in Sarcobatus replacing native grasses.

Forested wetlands. A number of Rocky Mountain tree species can grow in wetlands, especially where the water table is high for only a portion of the growing season. Trees also occur in wetlands with a seasonally or permanently high water table on coarse-textured soils, for example, sandy and gravelly soils that have better aeration than finer textured soils. Trees usually are not present in deep snowbank areas, or even in the runoff zone below snowbanks. No tree species in the U.S. Rocky Mountains is restricted to wetlands. Species such as Larix laricina and Picea mariana occur abundantly in wetlands farther north in the Rocky Mountains of Canada. Populus angustifolia, P. balsamifera, P. trichocarpa, P. sargentii, P. acuminata, and Picea pungens, in many areas, are largely restricted to the riparian zone, a portion of which is usually wetland. For the most part, forested wetlands occur at springs and seeps and in areas with naturally high water table, including river floodplains. Two general types of forested wetlands are described here, those dominated by

coniferous tree species and those dominated by deciduous angiosperm tree species; the two types may integrade in many areas. All forest wetland types reported have mineral soils and fresh minerotrophic water sources. No forest wetlands have yet been described that occur on organic soils, and none have a saline or ombotrophic water source. In addition, nothing that could be described as true swamp, a forested wetland with permanent standing water, has yet been described, and it is highly probable that none occur.

a. Coniferous forested wetlands. High-elevation forests on level or gently sloping ground, especially where springs occur, may have seasonally or permanently high water tables. Timbering in wetlands, such as along stream courses in the Picea engelmannii - Equisetum arvense habitat type (the habitat type designation used in U.S. Forest Service studies describes the potential climax community of a site) in Idaho (Steele et al. 1983), can cause the water table to rise, which makes it difficult to re-establish tree seedlings (Daubenmire 1968). This illustrates that large transpiring plants, such as evergreen coniferous trees, can keep the water table low enough to allow self-propagation.

In Colorado's San Juan Mountains, the Mertensia ciliata - Abies lasiocarpa community occurs on rolling uplands, where water may be standing all summer (DeVelice et al. 1984). In northwestern Wyoming, Montana, central Idaho, and Utah, the Abies lasiocarpa - Calamagrostis canadensis community occurs at the margins of ponds, and represents the wettest stands in the Abies lasiocarpa series. Keammerer (1979) has described a Pinus contorta forest with wet understory from the Keystone Bog near Crested Butte, Colorado. Sphagnum spp. cover 55% of the ground surface, Carex aquatilis 35.3%, Carex canescens 3.7%, Deschampsia caespitosa 3.8%, Betula glandulosa 1.9%, Pinus contorta 8.5%, Vaccinium caespitosum 1.3%, and all other species 1.5%. This community is part of a bog complex described earlier.

b. Deciduous angiosperm forested wetlands. No record of wetland forests of this type has been found in the literature, but Populus tremuloides does occur on the margins of wetlands, such as ponds, and may dominate wetland communities. This species also occurs in gullies and depressions in grassland and Artemisia tridentata-dominated shrublands in some mountain parks and intermountain basins. The following habitat types may be wetlands: the Populus tremuloides - Heracleum sphondylium habitat type, which is common in Colorado (Bunin 1975; Boyce 1977; Hoffman and Alexander 1980) and Wyoming (Youngblood and Mueggler 1981); and the Populus tremuloides - Veratrum tenuipetalum habitat type, which occurs in Colorado (Hoffman and Alexander 1980).

Unvegetated wetlands with standing water. Wetlands that do not support vegetation are common in some mountain landscapes. They occur especially around the margins of lakes and reservoirs that have fluctuating water levels, in intermittent or temporary pond areas, on highly alkaline soils, and on disturbed sites. The conditions responsible for the lack of vegetation are various and important to observe because there is little information available about these types of wetlands.

Communities Adjacent to Running Waters

This group includes communities dominated by trees, shrubs, herbs, and mosses along streams and rivers in the Rocky Mountains. Although these communities are tied ecologically to river systems, and in most areas closely border the stream channels, they are not included as part of the Riverine System in the wetland classification of Cowardin et al. (1979). The adjacent running waters of these ecosystems provide them with a constant source of oxygen and minerals. The communities usually are flooded yearly and are subject to erosion and deposition flows. Water splashing from the channel is essential for maintenance of some characteristic plant species, and in many areas, the entire moss community.

The communities listed below are generally what are considered to be "riparian wetlands." They are, in many cases, dominated by "obligate riparian" species (sensu Dick-Peddie 1985); i.e., species found in the zone adjacent to running water or where soils are periodically saturated. The term riparian is not used here in a technical sense, but rather as a descriptive and characteristic Western term. The communities described below are those that appear to be obligate riparian.

The hydroperiod is a key external or forcing function that determines the vegetation composition and its productivity along running water systems. The intensity of flooding is as important as its frequency (Odum 1978).

Moss-dominated wetlands. Along many small high-gradient streams and around springs in the Rocky Mountains, communities dominated by mosses are common (Figure 54). The mosses may occur on rocks in and along the stream course, on bedrock walls of small canyons, or on soils along the stream side.

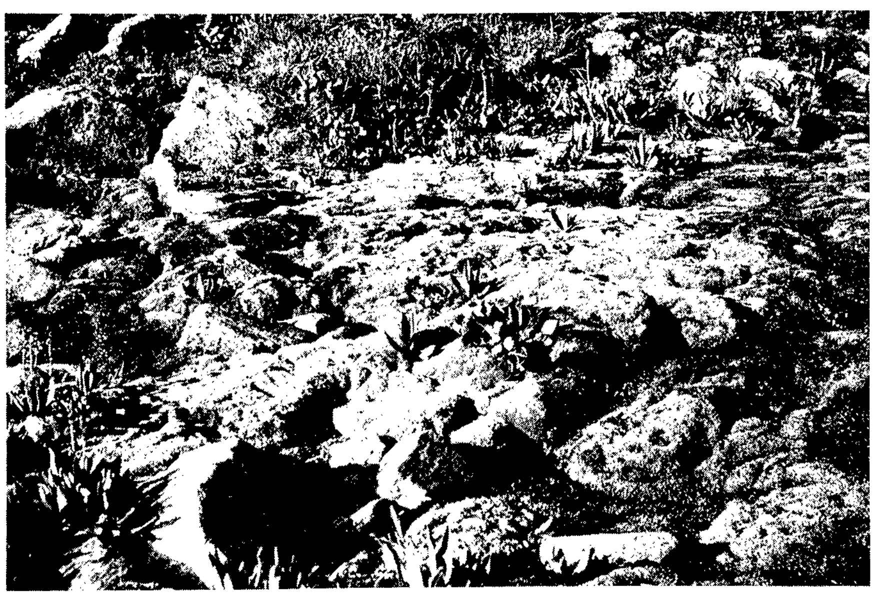


Figure 54. Moss-dominated community along permanently running water, near Flattop Mountain, Rocky Mountain National Park, Colorado, at 3,264 m (10,700 ft) elevation. (Photo by B. E. Willard.)

The best description of non-corticolous bryophyte communities is by Harthill (1968) from the Olympic Mountains of Washington. These byrophytes are restricted by floods from occurring along floodplains of large streams. The species that characterize the splash zone along streams in the Olympic Mountains include *Eurhynchium stokesii*, *Jamesonella autumnalis*, *Conocephalum conicum*, and *Mnium rostratum*.

No reports of moss communities from the Rocky Mountain Montane and Subalpine Zones were found in the literature review; however, personal observations indicate that they are widespread and usually define the width of the spray zone along streams. Communities dominated by species of the following genera will eventually be described: *Plagiomnium*, *Cratoneuron*, *Fissidens*, *Dichelyma*, *Fontinalis*, *Funaria*, *Hygrophypnum*, *Philonitis*, *Oncophorus*, and others. A number of herbaceous species often grow in the moss beds, such as *Saxifraga odontoloma*, *Cardamine cordifolia*, *Mimulus guttatus*, *Parnassia fimbriata*, and, of particular interest, the rare relictual Arctic species, *Chrysosplenium tetrandrum*.

Herbaceous wetlands. A number of wetland community types dominated by herbaceous species, such as grasses, forbs, and subshrubs, are common along water courses in the Rocky Mountains. Two general types are described: (1) herbaceous wetlands that typically occur along fast-moving, small mountain streams, and (2) herbaceous wetlands that occur on alluvial bars along water courses of any size. The latter category includes nearly barren gravel and sand bars that may be dry on the surface for much of the summer, yet saturated a short distance below the ground surface. These two categories of herbaceous wetlands appear to grade into each other and are most likely related along numerous successional pathways, most of which are still undescribed.

Along small streams in the Subalpine Zone wetland communities typically consist of a mixture of tall herbaceous flowering plants, such as *Mertensia ciliata*, *Senecio triangularis*, *S. serra*, *Mimulus lewisii*, *Heraculum sphondylium* ssp. *montana*, *Cardamine cordifolia*, *Delphinium barbeyi*, *Aconitum columbianum*, and other species (Figure 55). These communities are abundant throughout the Rocky Mountains, and may be the only wetland vegetation occurring along many small rushing streams. Floristic composition of these communities changes from north to south along the Rocky Mountain chain, with *Mimulus lewisii* and other Pacific Cordilleran species being abundant in the more maritime regions of Idaho, Montana, and northwestern Wyoming.

In the low Alpine-upper Subalpine Zones in Colorado's Front Range, the following herbaceous wetland communities have been described by Komarkova (1979): (1) *Primula parryi* - *Epilobium anagallidifolium*, (2) *Saxifraga odontoloma* -*Philonotis tomentella*, (3) *Trollius laxus* - *Erigeron peregrinus*, (4) *Cardamine cordifolia* - *Epilobium anagallidifolium*, (5) *Senecio triangularis* - *Stellaria umbellatus*, (6) *Mertensia ciliata* - *Adoxa moschatellina*, and (7) *Athyrium distentifolium*. Each community dominates a portion of the environmental gradient along streams.

Figure 55. Herbaceous wetland communities are characteristic of small high-gradient subalpine streams throughout the Rocky Mountains. This one, along East Cross Creek, Colorado, is dominated by Mertensia ciliata, Senecio triangularis, Cardamine cordifolia, and Heracleum sphondylium, ssp. montanum. (Photo by D. J. Cooper.)

Delphinium barbeyi is the dominant species along many high-elevation springs or running waters in Utah's Wasatch Plateau (Ellison 1954). This community is heavily impacted by domestic sheep, whose grazing and trampling has surely modified the floristic composition of stands. Other species occurring include Aster foliaceous, Erigeron ursinus, Senecio crassulus, Mertensia leonardii, Poa reflexa, and Artemisia discolor. Highly palatable species, such as Heracleum lanatum, Polemonium caeruleum, Osmorhiza sp., and Valeriana capitata, have been replaced by the less palatable species mentioned above, along with Achillea lanulosa, Rumex spp., and Chenopodium spp.

Herbaceous communities occurring at springs are poorly known in the Rocky Mountains, but would mostly likely be classified in this category.

A number of communities occur on nearly barren alluvium along river courses. Along Montana's Flathead River (Allen 1980), cobbly alluvium has communities dominated by Crepis elegans, while Oxytropis campestris dominates sandy alluvium. Other species occurring were Achillea millefolium, Dryas drummondii, Allium cernuum, and Heterotheca villosa. Dryas drummondii probably dominates communities in some portions of Montana, just as it does throughout its range farther north in Canada and Alaska. Epilobium latifolium is common on bare wet alluvium in moderately high-elevation areas throughout the Rocky Mountains (Figure 56). Agrostis hiemalis colonizes rocky areas and holds soil

Figure 56. A stream bed along the Las Animas River, in Colorado's San Juan Mountains, is dominated by Epilobium latifolium. (Photo by D. J. Cooper.)

on floodplains in Boulder Park, Colorado (Robbins 1918). Elymus glaucus dominates herbaceous washes on mesic sites adjacent to the North Fork of the Flathead River, high enough to escape annual inundation during the growing season (Allen 1980). While there has been considerable work on successional processes on moraines, floodplains, and other barren substrates in the sub-Arctic and Arctic, these investigations have been largely ignored in the Rocky Mountains.

Shrub wetlands. The most abundant shrub species occurring along running waters in the Rocky Mountains are Salix spp., Alnus tenuifolia, Betula fontinalis, and Swida sericea (Cornus stolonifera). Some species of Salix are pioneers on bare river alluvium, i.e., Salix glauca and S. planifolia in Boulder Park (Robbins 1918), but little specific information on this subject exists for the Rocky Mountains. Seeds of these shrubs are light and easily transported to suitable new habitats.

Betula fontinalis (B. occidentalis), and Alnus tenuifolia are the most abundant dominants along montane streams (Vestal 1914) (Figure 57). Streamsides dominated by this combination are reported from the Colorado Front Range (Vestal 1914), the Gunnison River in western Colorado (Lamborn 1962), the Grey's River region of Wyoming (Norton 1981), and in the Roosevelt and Arapahoe National Forests of Colorado (Hess 1981). Data from the four stands Hess sampled are presented in Table 30.

Figure 57. Betula fontinalis and Alnus tenuifolia are common dominant streamside species in the Rocky Mountains. (Photo by L. P. Rink.)

Hess' stands occurred along small mountain streams at 2,000 to 2,600 m (6,562 - 8,531 ft). The streambanks are inundated by spring runoff and this community, which has a closed canopy, is rarely greater than 10 to 15 m (32 - 49 ft) from the stream edge. Soils are alluvial and classified as Typic Haplaquolls, with a thick and dark A horizon that has a pH of 6.0 to 6.2.

Alnus occurs without Betula in the Big Cottonwood Canyon drainage, Utah (Allan 1962), in upper streamside communities in the Wasatch Mountains of Utah and Idaho (Ream 1963), along the Middle Blue River in Colorado (Giese 1975), along the Little Snake River, Wyoming (Quinlan 1980), on river islands in Garfield County, Colorado (WRD 1980b), and in the Salix bebbiana - Alnus tenuifolia association in New Mexico (Dick-Peddie 1985). Acer grandidentatum dominates similar communities in Idaho, Utah, and western Wyoming.

Alnus spp. roots have a symbiotic relationship with Actinomyces, which fix nitrogen, a valuable adaptation for plants colonizing barren river gravel habitats that have poorly developed soils. Other pioneers of bare gravels, such as Dryas drummondii, Eleagnus commutata, and numerous leguminous species, also harbor nitrogen-fixing bacteria. It would be of great value to understand more fully how other species, such as Agrostis hiemalis, Epilobium latifolium, and Salix spp., obtain nitrogen from bare gravel substrates.

Table 30. Stand data for a community dominated by Alnus tenuifolia and Betula fontinalis. (From Hess 1981.)

Species	Percent coverage (constancy)
Acer glabrum	4(100)
Alnus tenuifolia	37(100)
Betula fontinalis	26(100)
Salix sp.	29(50)
Salix bebbiana	10(50)
Salix lasiandra	6(50)
Salix scouleriana	3(50)
Ribes inerme	3(75)
Rosa woodsii	3(100)
Rubus strigosus	+(50)[a]
Bromus anomalus	+(50)
Calamagrostis canadensis	14(100)
Carex sp.	4(75)
Carex aquatilis	+(50)
Carex festivella	+(50)
Carex foenea	+(50)
Carex lanuginosa	7(50)
Juncus balticus	4(75)
Poa sp.	+(50)
Poa interior	+(50)
Poa pratensis	3(50)
Achillea lanulosa	+(50)
Agastache spp.	+(50)
Campanula rotundifolia	1(100)
Cardamine cordifolia	1(100)
Epilobium angustifolium	2(75)
Equisetum arvense	26(100)
Fragaria ovalis	1(50)
Galium boreale	1(50)
Habenaria sp.	+(50)
Haplopappus parryi	1(50)
Heracleum sphondylium	3(100)
Mentha arvensis	+(50)
Osmorhiza depauperata	2(75)
Oxypolis fendleri	1(50)
Potentilla sp.	+(50)
Rudbeckia lacinata	3(75)
Sidalcea candida	1(50)
Smilacina stellata	4(100)

[a]+ = presence, <1.

Alnus tenuifolia, Swida sericea, and Salix spp. can withstand flooding for periods of two growing seasons and can exhibit good adventive root growth during this period (Walters et al. 1980). Acer glabrum, Betula glandulosa, B. fontinalis, and Crataegus douglasii can tolerate flooding for most of one growing season, with some new root growth expected during this time. Rosa sp. and Symphoricarpos sp. are able to survive flooding for periods between one to three months during the growing season, but they produce few or no new roots during this time.

In New Mexico, the Salix irrorota - Cornus stolonifera (Swida sericea) community occurs near streamsides (Dick-Peddie, in prep.). In deep canyons along the eastern foothills of the Rocky Mountains, communities dominated by Corylus cornuta occur. In the foothills near Boulder, Colorado, Betula papyrifera occurs in this community type (Cooper 1984). Both Corylus and Betula papyrifera are eastern U.S. species that are Pleistocene relicts along the Rocky Mountain Front Range. Viburnum edule and Aralia nudicaule, relict shrubs in the Rockies, grow in a wetland on the northfacing slope of the Big Thompson River in Rocky Mountain National Park at 2,608 m (8,550 ft) elevation. This stand also contains several Pleistocene relict herbs (Willard 1985).

Forested wetlands. Forests line many streams and rivers in the Rocky Mountains. In many places, this vegetation defines the "riparian" strip, or corridor, which in some areas forms the most abundant wetland vegetation. This is especially true in the Foothills and Montane zones, where steep topography creates rapid runoff and complete drainage, and in many of the drier intermountain basins and mountain parks.

Coniferous trees are more abundant at higher elevations, whereas deciduous trees usually dominate at lower elevations. The composition of streamside communities forms a continuum of change in the Wasatch Mountains of Utah and Idaho (Ream 1963). Lower elevation streamside communities are dominated by Populus angustifolia and Acer negundo, whereas comparable higher elevation streamside communities are dominated by the shrubs Salix spp. and Alnus tenuifolia. In the Big Cottonwood Canyon drainage in Utah's Wasatch Mountains, the lower montane at 1,525 - 1,983 m (5,000 to 6,500 ft) elevation is dominated by Populus angustifolia, Betula fontinalis, and Swida sericea. The midmontane belt, at 2,074 - 2,440 m, (6,800 to 8,000 ft) is dominated by Picea pungens, Salix drummondiana, S. pseudocordata, and S. exigua. The upper montane belt, at 2,440 - 2,896 m (8,000 to 9,500 ft) is dominated by the shrubs Alnus tenuifolia and Salix spp., especially Salix scouleriana.

In the Rocky Mountains, the wettest sites are usually occupied by Populus angustifolia, P. balsamifera, P. tremuloides, Salix spp., Alnus tenuifolia, and Rubus sp. (Walters et al. 1980). At lower elevation in the southern Rocky Mountains, the successional trend reported by Walters et al. (1980) is from Populus angustifolia toward a climax dominated by Picea pungens. Populus angustifolia, however, occurs at lower elevations than Picea pungens in many areas.

No Rocky Mountain tree species can withstand flooding for periods of two or more consecutive growing seasons (Walters et al. 1980). Abies amabilis, Picea engelmannii, P. glauca, P. pungens, Populus angustifolia, P. balsamifera, P. tremuloides, P. trichocarpa, Thujaplicata, and Tsuga heterophylla can withstand flooding for most of one growing season and still produce some new root development. Abies concolor, A. grandis, A. lasiocarpa, Acer negundo, Pinus contorta, P. monticola, P. ponderosa, and Pseudotsuga menziesii are able to survive flooding for periods of 1 to 3 months during the growing season, but will produce few new roots or will be dormant during the flooded period.

At present, great blue herons (Ardea herodias) nest in Colorado, primarily in Populus angustifolia and P. tremuloides, along river systems in Moffat, Routt, and Jackson Counties (Torres et al. 1978).

a. Coniferous forested wetlands. A number of forest types dominated by coniferous tree species occur on floodplains and terraces. Although they appear to benefit from the moisture of the floodplain, they are not dependent upon running water. In many areas, Picea pungens is closely confined to river floodplains of permanent streams, such as along Colorado's Blue River (Giese 1975).

In the southern Rocky Mountains, the Picea engelmannii - Heracleum sphondylium, Picea pungens - Poa pratensis, and Picea pungens - Swida sericea habitat types occur along streams, on floodplains and terraces, and at springs (DeVelice et al. 1984).

The Picea engelmannii - Equisetum arvense habitat type occurs on saturated soils of stream terraces in eastern Idaho and western Wyoming (Steele et al. 1981). Streptopus amplexicaulis, Parnassia fimbriata, Senecio triangularis, and other hydrophytes also occur. This habitat type forms the climax, or stable, forest along the North Fork of the Flathead River, Montana (Allen 1980), and also occurs along Cross Creek in Colorado's Sawatch Range (Figure 58) (Cooper 1986). Here, as in similar stands in the Colorado Rockies, Equisetum arvense can be a codominant.

The Picea engelmannii - Caltha leptosepala habitat type occurs on terraces from 2,499 to 2,896 m (8,200 - 9,500 ft) elevation in eastern Idaho and western Wyoming (Steele et al. 1981). Trollius laxus, Mitella pentandra, Senecio triangularis, Saxifraga odontoloma, Kalmia polifolia, Vaccinium occidentalis, and Phyllodoce empetriformis may occur as understory. In Utah's Uinta Mountains, this habitat type occurs near springs and seeps, where there are clay- and organic-rich soils. Calamagrostis canadensis, Carex atrata, and Deschampsia caespitosa are abundant. This habitat type provides important resting and feeding ground for elk. It is closely related to the Abies lasiocarpa - Caltha biflora habitat type, which occurs in the northern Rocky Mountains on perpetually saturated organic soils to approximately 30 cm (11.8 in) depth, with pH ranging from 5.3 to 6.1.

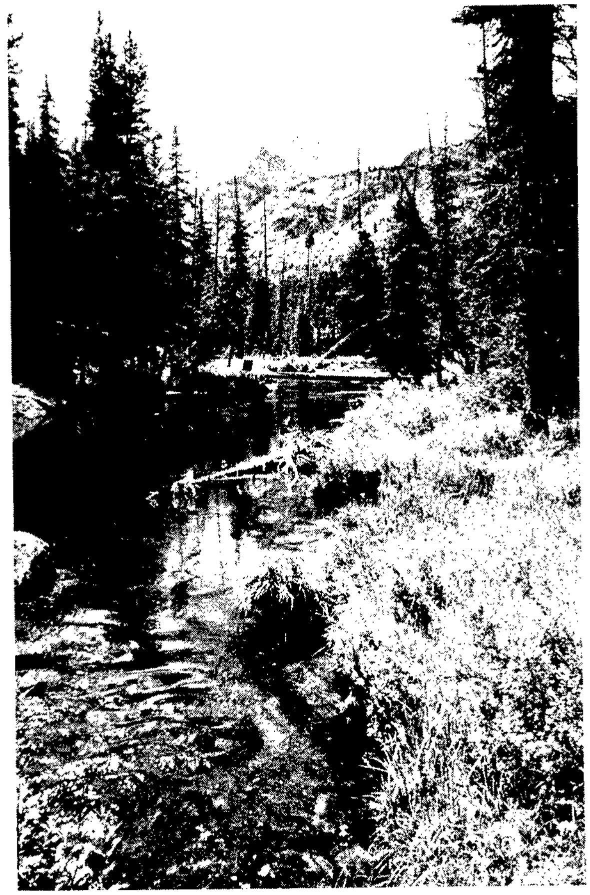


Figure 58. Picea engelmannii - Equisetum arvense habitat type along Cross Creek, Sawatch Range, Colorado. The water table is within 30 cm of the ground surface in these stands. (Photo by D. J. Cooper.)

The Abies lasiocarpa - Streptopus amplexicaulis habitat type occurs in both the northern Rockies and Utah's Uintah Mountains (Mauk and Henderson 1984; Steele et al. 1981) adjacent to smaller stream courses or springs on steep slopes at mid-elevation. Mertensia ciliata, Saxifraga odontoloma, Senecio triangularis and other species are common.

The Abies lasiocarpa - Calamagrostis canadensis habitat type occurs on streamsides in Utah's Uintah Mountains (Mauk and Henderson 1984) and, in Yellowstone National Park, Wyoming, it occurs along lake shores and on stream terraces (Steele et al. 1981). This habitat type has three phases in Wyoming, characterized by Ledum glandulosum, Vaccinium cespitosum, and Calamagrostis canadensis, respectively. Stands dominated by Vaccinium cespitosum are characteristic of snowbeds at and just below treelimit throughout the Colorado Rockies.

The Picea engelmannii - Carex disperma habitat type occurs in eastern Idaho and western Wyoming on saturated soils with an organic layer up to 30 cm (11.8 in) thick (Steele et al. 1981).

In New Mexico (Dick-Peddie, in prep.), two habitat types occur in the Subalpine riparian-blue spruce series along mountain streams: (1) Picea pungens - Amelanchier utahensis - Swida sericea - Carex spp. and (2) P. pungens - Poa pratensis. In New Mexico, the blue spruce-narrow-leaf cottonwood series also occurs along streams: (1) Picea pungens - Populus angustifolia - Alnus tenuifolia and (2) P. pungens - P. angustifolia - Amelanchier utahensis - Salix spp. - Carex spp.

b. Deciduous angiosperm forested wetlands. Populus spp.-dominated communities are present along most mountain rivers in the Rocky Mountains (Figure 59). Community dominance shifts from Populus deltoides (P. sargentii) to P. acuminata to P. angustifolia (Marr 1967) with increasing elevation in the southern Rocky Mountains. In western Montana, P. trichocarpa or P. balsamifera may be the dominant cottonwood species and, in New Mexico, P. fremontii may be dominant. Populus balsamifera is most likely a Pleistocene relict in the southern Rocky Mountains; in Colorado it is found along streamsides and sometimes other wet sites. It occurs in scattered stands as far south as Gunnison. Acer negundo is widespread, but limited primarily to lower elevations. In the far southern Rocky Mountains of southern New Mexico, a number of hardwood tree species endemic to that area occur along streams, including Alnus oblongifolia, Juglans major, J. microcarpa, and Platanus wrightii.

Figure 59. Populus angustifolia dominates streamside floodplains in many portions of the Rocky Mountains. Shown here is the Animas River in southwest Colorado. (Photo by D. J. Cooper.)

In New Mexico, the narrow-leaf cottonwood series includes four community types (Dick-Peddie, in prep.): (1) *Populus angustifolia* - *Poa pratensis*, (2) *P. angustifolia* - *Forestiera neomexicana*, (3) *P. angustifolia* - *Amelanchier utahensis*; and (4) *P. angustifolia* - *Salix irrorata*. The narrow-leaf cottonwood-mixed deciduous series includes: (1) *Populus angustifolia* - *Alnus oblongifolia* - *Acer negundo*, (2) *P. angustifolia* - *Juglans major*, and (3) *P. angustifolia* - *P. fremontii* - *Alnus oblongifolia*. At lower elevations, the broadleaf cottonwood series occurs: (1) *Populus acuminata* - *P. fremontii*, (2) *P. fremontii* - mixed shrub-mixed grasses - forbs, (3) *P. fremontii* - *Acer negundo* - *Cornus stolonifera* (*Swida sericea*).

At low elevations in Colorado, *Populus angustifolia* occurs with *Salix exigua*, e.g., in Glenwood Canyon of the Colorado River (De Leuw, Cather and Company 1977), in the Roosevelt and Arapahoe National Forests (Hess 1981), and in the San Luis Valley (Ramaley 1942). *Populus angustifolia* occurs with *Amelanchier utahensis* in Glenwood Canyon and other parts of Colorado. *Populus angustifolia* occurs with *Lonicera involucrata* in northern Colorado (Robbins 1910) and in Summit County (Klish 1977).

In Montana, along the North Fork of the Flathead River (Allen 1980), *Populus trichocarpa* dominates deciduous forest communities. It occurs in a midsuccessional stage in floodplain development with *Senecio pseudaureus*, *Vicia americana*, and *Elymus glaucus*. *Populus trichocarpa* occurs as a mid-successional stage with few shrubs, and the *P. trichocarpa* - *Swida sericea* community occupies deep soils.

Unvegetated wetlands. Wetlands that do not support vegetation are common along some rivers and streams in the Lower and Upper Montane Zones. They occur as river bars composed of sand, silt, and gravel; barren bedrock outcrops can also occur. They also occur where bank vegetation has been eroded away by flooding and has not yet re-established.

Communities in Running Water

This category of wetlands, including periphyton, aquatic moss, and other instream communities, is omitted from this report because it is generally considered aquatic, although Cowardin et al. (1979) include the edge of some streams as wetlands. The various ecosystems resulting from beaver dams on running waters are described under fens, fresh water marshes, and shrub wetlands.

3.4 SUCCESSIONAL RELATIONSHIPS

The idea that wetland communities are successional is almost as old as American ecology. In 1916, F. E. Clements (Clements 1916) described succession as the development of the climax. To Clements, all wetlands were seral, even wetlands that are obviously long-lived, such as Florida's Everglades or southern cypress swamps, which he termed serclimax. The most prominent early American textbook on plant ecology by Weaver and Clements (1938), popularized hydrarch succession, which in their view progressed from a barren lake, to communities dominated by unattached floating or rooted submerged species, to rooted floating-leaved species, to rooted emergent species, eventually leading to a climax terrestrial community. This focus of American ecologists on the dynamic changes in vegetation accompanying changes in physical features (Figure 11, Chapter 1) evolved from classical work by Cowles (1899) and Clements (1905), which set the stage for much of the ecological research during that period (Shelford 1907, 1911; Cooper 1912, 1923).

Almost all ecological research on Rocky Mountain wetlands during the first three decades of the 20th Century described communities as part of a primary successional sequence leading to a mesic terrestrial climax. In 1908, Ramaley and Robbins (1909) described the vegetation of Redrock Lake in the Colorado Front Range as having sharply marked zonation. They published a vegetation map (Figure 60) showing concentric banding around the lake and depicted the zones on profile view drawings (Figure 61). The zones included a lake zone, sedge zone, shrub zone, and Engelmann spruce zone; each succeeding zone was dominated by larger plant species. The vegetation map gives a real feeling of vegetation encroaching upon the lake; succession in action.

Several other studies at that time, including Robbins (1918), Ramaley (1919), Vestal (1914), and Reed (1917) also described successional vegetation along streams and around lakes elsewhere in the Colorado Rocky Mountains. Robbins (1918) provided cross-sections of wetland vegetation in Boulder Park from the rooted submerged zone through the herbaceous meadow zone (Figure 62). He diagrammed not only hydroseres, but also xeroseres, on gravelly, sandy, and silty floodplains and on glacial terraces (Figure 63).

According to Ramaley (1919), the successional relations of lakeside communities are a straight-forward hydrarch series (succession). Changes in soil moisture conditions lead directly to change in vegetation from pond to spruce forest through a series of communities. Silt and plant debris build the level of the soil relative to that of the water. Sediment can be deposited by stream overbank flow or deltaic deposits where they enter stagnant water. Some sediment is also deposited by slopewash during spring snowmelt or heavy rains. This sediment is derived from weathering and erosion of bedrock and soils in the surrounding uplands. Disturbance of upland soils can create a source of sediment that is eventually deposited in the depressions and valleys. Accumulated organic material brought in by water and wind, and then settling to the lake bottom, augments the sediments.

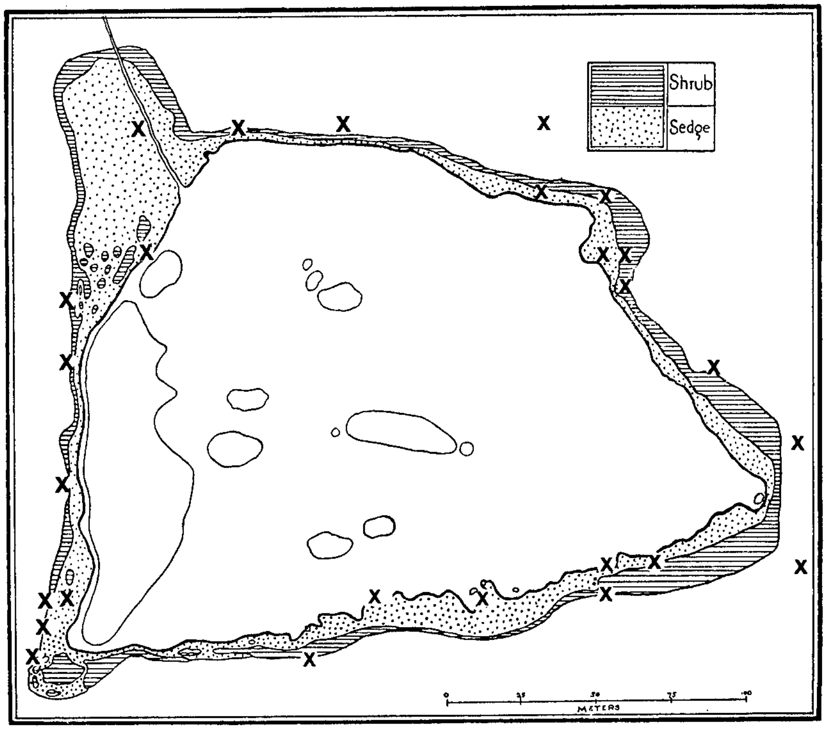


Figure 60. Map of Redrock Lake, Colorado, showing plant zones. (After Ramaley and Robbins 1909.) Circles areas in the lake are groups of water lily leaves; dotted areas represent sedges; horizontal shading represents shrubs. Outside of the shrub zone is forest, the exact character of which is discussed in the account of zonation. The X's indicate stakes or stations used in making the survey.

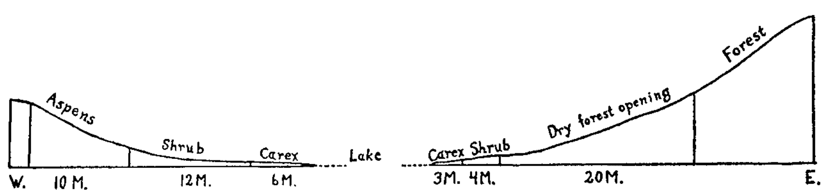


Figure 61. East-west profile of Redrock Lake, Colorado. (From Ramaley and Robbins 1909.). The greater width of the sedge and shrub zones on the west is accounted for by the fact that there is a considerable amount of seepage water through the low aspen-covered moraine from the wet meadow to the west, and that the prevailing west wind compresses the vegetation along the east shore.

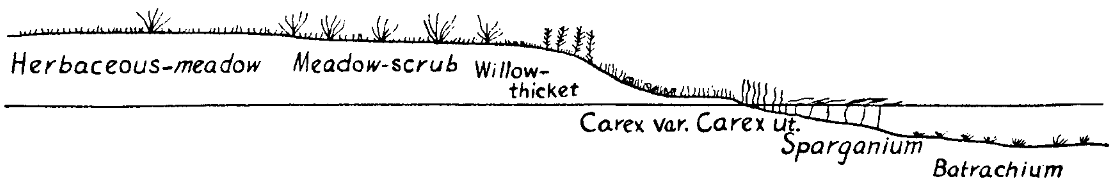


Figure 62. Cross-section of west shore of Park Lake, Boulder Park, Colorado. (From Robbins 1918.) "Carex var." is Carex aquatilis; "Carex ut." is Carex utriculata; Batrachium = Ranunculus (in part).

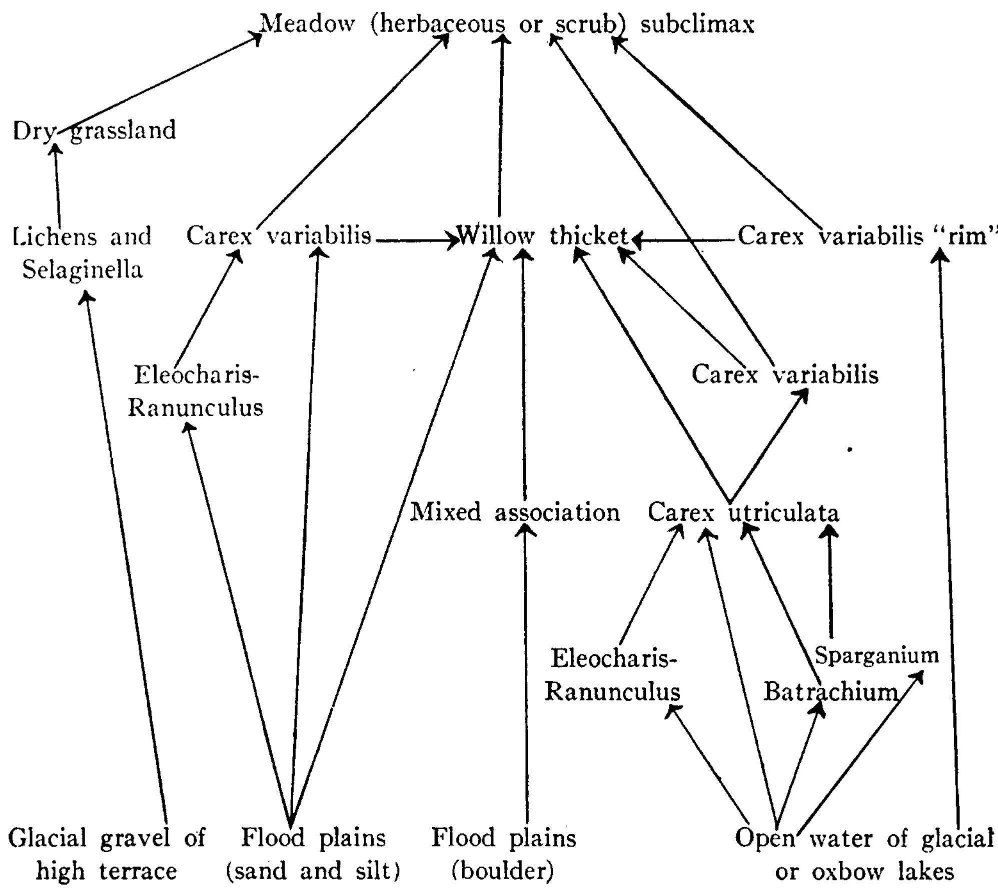


Figure 63. Diagram of plant succession, Boulder Park, Colorado. (From Robbins 1918.) Carex variabilis = C. aquatilis, Batrachium = Ranunculus (in part).

Successions that create new soil surfaces, such as filling in a lake or development of vegetation on a barren gravel bar, are primary successions. This is a slow process that requires many centuries to reach a stable or climax community. Secondary succession occurs after a disturbance alters or destroys the vegetation cover, but does not destroy the soil, for example, a flood or fire that destroys a streamside forest. Regeneration of the forest (secondary succession) usually happens quickly, unless subsequent erosion removes the soil down to bedrock. However, a fire in a fen may burn enough peat to create a pond during wet seasons and initiate primary succession.

Around Rocky Mountain lakes and along streams, wetland plant species and communities may form distinctive belts that may remain relatively stable, undergo cyclical fluctuations, or encroach upon one another, depending upon annual changes in water table; stream, ice, or wind erosion; fire; flooding; animal use patterns; sedimentation; and fluctuations in weather.

The time function for successional processes varies greatly, depending upon the type, location, and origin of the wetland. The Redrock Lake setting photographed and published with the Ramaley and Robbins study (1909) was rephotographed in 1972 by Reid (1972) to examine vegetation stability over the elapsed 64 years (Figure 64). Vegetation had noticeably advanced into the lake in some areas, while in other areas, virtually no advance had occurred. The oldest peat in Redrock Lake, which has no inlet or outlet, has been carbon dated as 6,900 years old (Pennak 1963), yet the lake is not filled. Many Rocky Mountain lakes, such as moraine-dammed lakes in major river valleys, have been entirely filled by water-deposited sediment and organic matter since the last stage of the Pleistocene glaciation (Figures 65, 66).

Some beaver ponds silt in within dozens to hundreds of years (Figure 67), yet a kettle pond dated by Pennak had accumulated only 175 cm (69 in) of peat in 6,190 years (Pennak 1963). In Montana's Madison Range, Patten (1963) considered that the vegetation was still adjusting to the post-Pleistocene climate, but that vegetation patterns, including mountain meadows, are relatively stable. Mountain meadows in the Cascade Range (Franklin et al. 1971) and the Olympic Mountains (Kuramoto and Bliss 1970) of Washington are the result of forest disturbances, and are successional.

Rivers at the middle elevations in the Rocky Mountains flow in valley bottoms or across sediment-filled lake-beds (Figures 65, 66), and the channels are relatively permanent. Unless stream gradient changes, these river floodplains may be permanent wetlands. Wetlands associated with fast-moving mountain streams, such as those dominated by *Betula fontinalis*-*Alnus tenuifolia* or *Senecio triangularis*-*Mertensia ciliata*, also do not show successional trends.

A number of successional pathways have been described for Rocky Mountain wetlands. Hydrosere stages leading from pond to mesic terrestrial communities are described by Reed (1952) for the Jackson Hole, Wyoming, area, by Robbins (1918) for Boulder Park, and by Ramaley (1920) and Reed (1917) for northern Colorado. The Jackson Hole and Boulder Park successions start with submerged species dominated especially by *Ranunculus aquatilis* (*R. tricophyllus*), *Potamogeton* spp., *Utricularia vulgaris*, and *Sparganium angustifolium*. The

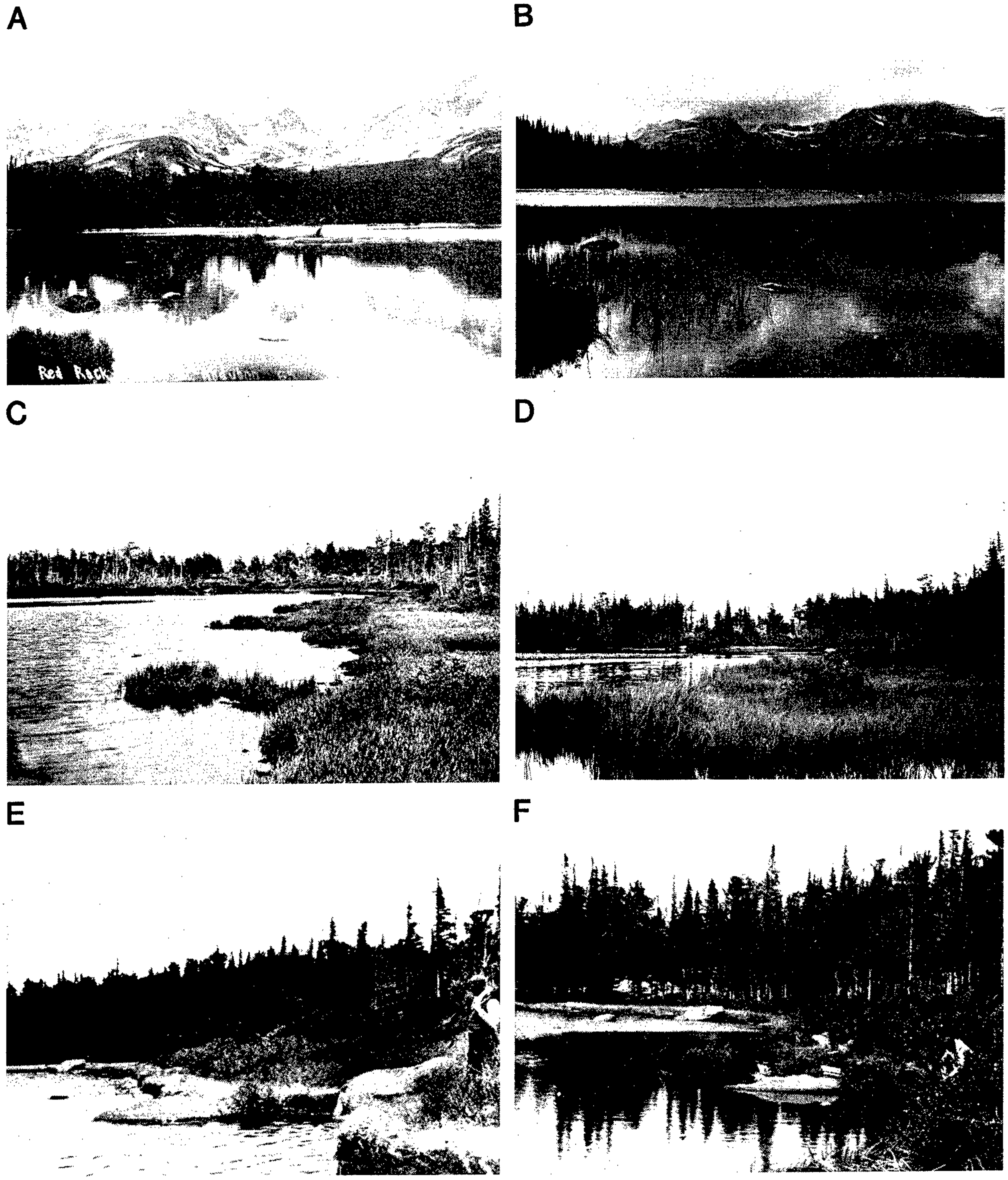


Figure 64. Comparative photographs of Redrock Lake, Colorado, 3,050 m (10,000 ft) elevation. (From Ramaley and Robbins 1909 and Reid 1972.) Three views are compared over this 64-year time span. Photos A, C, and E, above left, were taken in 1909, and B, D, and F, above right, were taken in 1971. Photo B shows sedges have invaded the open water toward the two rocks in the left foreground where no emergent sedges were present in Photo A. Photo D shows encroachment of sedges onto the lake, changing edge configuration from Photo C. There is little apparent change between Photos E and F, except an increase in shrubs in the latter photo.

Figure 65. View of the Kawuneeche Valley on the North Fork of the Colorado River, Rocky Mountain National Park, Colorado, shows distinct borders of valley bottom wetlands. This valley is along a fault zone; the wetland complex extends more than 17.3 mi, ranges from 0.5 to 1.4 km (0.3 to 1.6 mi) in width, and from 2,855 to 2,562 m (9,360 to 8,400 ft) elevation. (Photo by B. E. Willard.)

Figure 66. Horseshoe Park, Rocky Mountain National Park, Colorado, showing how level the surface of filled glacial lakes can be; 2,593 m (8,500 ft) elevation. (Photo by B. E. Willard.)

Figure 67. The beaver pond shown in the foreground was abandoned in 1955, and had filled in when this photograph was taken in 1958. Hidden Valley, Rocky Mountain National Park, Colorado, 2,715 m (8,900 ft) elevation. (Photo by B. E. Willard.)

second stage at Jackson Hole includes free-floating Lemna spp. and rooted floating-leaved Nuphar polysepalum and Ranunculus natans, whereas these species are absent in Boulder Park. Third is a rooted emergent stage dominated by Carex spp., Glyceria spp., Eleocharis spp., and Ranunculus spp. The Jackson Hole successional sequence was taken no further. The fourth stage in Boulder Park is on mud and is dominated by Alopecurus aequalis. The fifth stage in Boulder Park and the first stage in northern Colorado lakes successions are dominated by Carex aquatilis. The Boulder Park succession ends at a stage dominated by Carex festivella, but in northern Colorado, willow moor, dominated by Salix plainfolia and S. glauca, develops, followed by a rush moor dominated by Juncus drumondii, a meadow moor, a heath association (with Kalmia polifolia and Gaultheria humifusa), a meadow, and, finally, a conifer forest--a total of eight seres in all. In temporary ponds in Oregon's Willamette Valley at low elevation, the following zones or stages occur: submerged, floating-leaf, reed-swamp (Typha latifolia), sedge (Eleocharis palustris), meadow, willow, cottonwood, and grassland (Lippert and Jameson 1964)--quite similar to some Rocky Mountain stands.

Along the North Fork of the Flathead River in Montana (Allen 1980), there are five general stages of flood-plain succession. The first, a pioneer stage, may begin as a cobble wash, a harsh and highly disturbed environment dominated by Crepis elegans, Agrostis alba, Oxytropis campestris, and Dryas drummondii, or on deep fine sand pockets where Oxytropis campestris occurs with Allium cernuum. In old ephemeral channels, oxbows, and sloughs, where

there is ephemeral inundation and increased silt and clay, communities occur that are dominated by *Juncus tenuis*, *Agrostis alba*, *Poa palustris*, and *Equisetum arvense*. In the most mesic sites, adjacent to the river but high enough to escape annual inundation during the growing season, communities occur that are dominated by *Elymus glaucus*, *Poa palustris*, *Phleum pratense*, and *Solidago canadensis*. The second stage is the early successional stage, dominated by *Populus trichocarpa* and *Salix* spp. The third stage, the mid-successional stage, leads to the development of a tall *Populus* forest with a dense understory of *Senecio pseudaureus*, *Aster* sp., *Vicia americana*, *Taraxacum officinale*, and *Elymus glaucus*; a *Populus* - *Cornus stolonifera* community develops on deep soils. *Picea engelmannii* and *P. glauca* invade at this stage. During the fourth, late successional stage, *Picea engelmannii* and *Populus trichocarpa* are codominant. The fifth stage is a stable climax *Picea engelmannii* - *Equisetum arvense* community. These stands and stages form a continuum of successional seres that are seemingly perpetuated by periods of erosion and deposition associated with flooding.

Several successions are described that have three species dominating each of three successive stages: *Carex utriculata*, *C. aquatilis*, and *Calamagrostis canadensis* (Wilson 1969; Cooper 1986). In Rocky Mountain National Park, streamside wetland succession begins with *Carex aquatilis*, which traps clay and develops a perched water table (Wilson 1969). The succession then proceeds to *Carex utriculata* and then to *Calamagrostis*. Lakeside successions in the same area begin with *Carex utriculata*. A similar sequence is observed along Cross Creek in the Sawatch Range, Colorado (Cooper 1986).

In eastern Canada, similar successional stages to these occur with floating *Nuphar* spp. followed in succession by *Carex utriculata*, *Calamagrostis canadensis*, woody shrubs, and spruce forest (Dansereau and Segadas-Vianna 1952). In Canada, however, the spruce forest usually includes a type of bog dominated by *Sphagnum* and black spruce (*Picea mariana*). Similar successions also occur in Britain (Walker 1970), where Tansley (1939) found that the successional step beyond carr depends upon climatic conditions, specifically temperature and precipitation. In cool areas of high humidity, carrs develop into raised bogs; however, in areas where moisture is not as abundant, succession produces a mesophytic forest:

$$\text{water} \rightarrow \text{fen} \rightarrow \text{carr} \begin{cases} \nearrow \ \text{bog} \\ \searrow \ \text{mesophytic forest} \end{cases}$$

In Canada, wetlands may change in a sequence from marsh to fen to bog; in some areas bog will develop into swamp, but in other areas swamps may develop into bogs (Zoltai et al. 1975). In Alaska, succession in ponds and on river floodplains leads from a pond or gravel bar to a mesic spruce forest. But forest shading and insulation promotes the development of permafrost with a shallow summer thaw depth; then a bog, which is the climax vegetation, develops in a "retrogressive succession" (Drury 1956; Viereck 1970).

The potential climax community for hydroseres with nearly identical early successional stages differs from region to region. From information currently available, it appears that the Rocky Mountain climate is too continental to allow extensive bog development, therefore successions end with mesic well-drained forests.

Stream meandering in Colorado mountain valleys erodes floodplain soils, interrupting floodplain aggradation and secondary succession in the Cross Creek Valley in Colorado's Sawatch Mountains (Cooper 1986). In Colorado's upper Laramie River Valley, flood scouring creates bare alluvial plains upon which develop dry or mesic carr types as shown in Figure 68 (Phillips 1977). Beaver move into the stream sections to feed on willows, and their dams pond water in portions of the new stands. The pond is colonized by sedges (Carex aquatilis and C. utriculata are dominants), which form fens. Eventually, Salix planifolia colonizes the fen, forming a high humification type carr. If this succession proceeds undisturbed by river flooding and scouring, accumulations of organic matter from willows, Hypnaceae mosses, and sedges may raise the ground above the water flush level. Paludification occurs and a barely humified surface develops, which suggests bog development. Succession rarely proceeds this far before it is interrupted by flooding or fire.

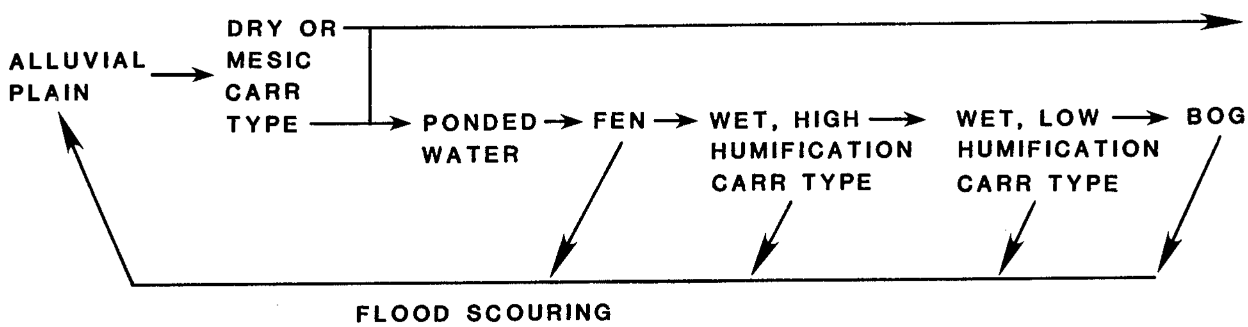


Figure 68. Upper Laramie River wetland secondary succession processes. (From Phillips 1977.)

In Rocky Mountain National Park, Colorado, a single community type (e.g., the Carex utriculata community) may be represented by both stable and successional stands (Wilson 1969). Aggradation is occurring in some stands, driving succession, but in other stands oxidation and erosion keep aggradation in balance.

Some researchers feel that vegetation produced as a result of disturbance, i.e., severe flood, fire, drought, or overgrazing, will persist if the disturbance persists, and vegetation will change (succession) when disturbance ceases (van der Valk 1982). Theoretically, there is a progressive increase in the stability of successional stands that follow one another in time on one site, because there is a decrease in both the kinds and magnitudes of changes (Marr 1967). It seems as though disturbance processes that occur constantly,

such as stream-caused erosion-deposition cycles and solifluction on mountain slopes, are fundamentally different from infrequent cataclysmic events, such as forest fires or damming of streams by beaver. Moderate disturbance regimes are normal, and even essential, processes for maintaining the climatic climax (sensu Marr 1967) in many ecosystems and biomes. Elimination of the disturbance regime in these ecosystems will initiate succession. This is true for grasslands (elimination of fire or grazing) and may be for some types of wetlands as well. Stream meandering is a normal process for rivers and streams in balance with local climate and geology, just as overbank sediment deposition and primary production are. Therefore, it may be justifiable to consider many Rocky Mountain wetlands a type of climax, not successional.

Lakes in Oklahoma that have fluctuating water levels do not have a sequence of lakeshore communities that would eventually give rise to climax vegetation (Penfound 1953). Instead, communities that develop are usually eliminated by subsequent change in the water level and succession does not occur. Whether or not this occurs in Rocky Mountain lakes is not known. Fire has been documented in one California Sierra Nevada fen (Erman 1976), although fire probably only occurs during drought periods. The effect of fire is rapid oxidation of peat and lowering of the ground surface relative to the water table, thus reversing successional trends.

The question of whether shallow water plants with different life forms overlap, or form distinct zones in lakes, has received considerable research. According to Odum (1971), it should not be assumed that all three zones (floating, rooted submergent, rooted floating) will be present or arranged in the order expected in any given body of water. In Colorado high mountain lakes, any of these zones may be entirely lacking due to absence of appropriate flora, excessive wave action, and possibly lakes freezing to the bottom. Large, emergent species, such as Typha spp. and Scirpus spp., are also lacking in many higher elevation areas, but they often are replaced by various Carex spp.

In New York's Chautauqua Lake, zones appear discrete to the eye, but considerable overlap between life forms occurs. For example, floating-leaf species occur with emergent species, and submerged rooted species occur in all zones (Nicholson and Aroyo 1975). The authors describe four vegetation zones based on depth of water: (1) submerged at 1.0 - 1.75 m (3.3 - 5.7 ft), (2) outerfloating leaf at 1.0 - 1.1 m (3.3 - 3.6 ft), (3) emergent at 0.6 - 0.9 m (2.0 - 3.0 ft), and (4) inner-floating leaf at 0.5 - 0.6 m (1.6 - 2.0 ft). A sudden change between life forms is seen only between the floating-leaved and emergent vegetation. This is caused by Pontederia cordata, a broadleaf emergent, which is superior in its ability to fix and accumulate biomass, stabilize the physical environment, and restrict the abundance of other species, which eliminates some species, but allows others to survive. Thus, succession does not always lead directly from one life form to the next, but instead life forms may grade into one another.

Primary production increases in hydrarch succession up to and including the emergent stage, beyond which production decreases significantly (Westlake 1963). In oxbow ponds in central Alberta, Canada, production of the rooted

submerged community was 200 g/m^2, the emergent community was 465 g/m^2, and the meadow community was 325 g/m^2 (van der Valk and Bliss 1971). Production in these ponds increased in steps as a new life form, which is more massive, came into dominance, producing a sudden change.

Numerous factors can initiate succession in terrestrial communities or change the direction of succession in wetlands. In Colorado's Monte Vista Wildlife Refuge in the San Luis Valley, native vegetation was irrigated to increase waterfowl habitat. In areas with saline soil, Sarcobatus vermiculatus has replaced both native grasses and Chrysothamnus spp. (Enright 1971). In wetter areas, Sarcobatus and Distichlis stricta were replaced by Juncus balticus, Carex spp., and Eleocharis spp., whereas in the wettest areas Typha latifolia, Scirpus spp., and Calamagrostis spp. increased markedly (Posphala 1969; Robinson 1971). In the Canadian prairies, a water table rise in a mesic prairie community increased the salt content of soils (Keith 1958) and the prairie was replaced by Hordeum jubatum, and then by Distichlis as the salt content and water table increased further. In the Indiana Dunes National Lakeshore, Typha spp. invaded a wetland complex dominated by Carex stricta and Calamagrostis canadensis after the water level was elevated (Wilcox et al. 1985). Cattail coverage changed from 2.0% to 37.5%, while sedge-grass coverage changed from 56.4% to 5.7%, between the years 1938 and 1982.

Some investigators have hypothesized that grazing by domestic livestock in wetlands has caused species composition change. For example, Juncus balticus is not grazed by cattle in Montana and Pierce (1982) considers it an increaser. Stands presently dominated by J. balticus were dominated by other species in the past. On Utah's Wasatch Plateau, sheep grazing has eliminated the desirable forbs along streams and other wetlands (Ellison 1954). At present, unpalatable species, such as Delphinium barbeyi, dominate these wetlands.

In some types of wetlands, a key to predicting vegetation change is a knowledge of the potential flora of wetlands (as determined by the soil seed bank and other potential seed sources) and life history characteristics of species in the vegetation (Harris and Marshall 1963; Pederson and van der Valk 1984). Important life history characteristics are: (1) potential life span, (2) propagule longevity, and (3) propagule establishment requirements (van der Valk 1981). This information will help determine how each species responds to changes in the physical-chemical environment, competition, herbivory, and disease.

According to Marr (1967), it is relatively easy to see that a successional stand is unstable, i.e., that it is not in equilibrium. Stands that are climax will be dominated by the same species of plants for a period of time that is long in comparison with the average life span of single individuals of those species (Beadle and Costin 1952), e.g., more than 1,000 to 1,500 years for Picea engelmannii forests in the Colorado Subalpine Zone.

In summary, Rocky Mountain wetlands are diverse, complex, dynamic systems. Generalizations regarding successional status of wetlands, or even a single wetland community type, will not apply everywhere. Some communities will clearly be successional, whereas others may rarely be successional. An important difference between mountain and lowland ecosystems is that because chemical rock weathering is very slow and annual primary production is small in high mountains, rates of pond filling, floodplain aggradation, and organic matter accumulation in many areas may be very slow. Even though change can be predicted for a specific site, it may take thousands of years in cold mountain regions, whereas similar ecological changes may occur in dozens or hundreds of years in warmer low-elevation regions. Application of climax and successional concepts for many communities will depend upon the region in which the investigation takes place, the type of wetland being studied, and the investigators' own concepts of time and rate of process.

CHAPTER 4

ECOLOGICAL PROCESSES IN ROCKY MOUNTAIN WETLANDS[1]

4.1 INTRODUCTION

This chapter focuses on factors that regulate nutrient cycling and productivity in Rocky Mountain wetlands. Investigations done in the Rocky Mountains are few; therefore, much of the information presented here is based on studies of high-altitude and cold-climate freshwater wetlands from other parts of the world. Although process rates and plant species may differ, investigations of other wetland systems, together with the relatively limited Rocky Mountain studies, provide a clearer understanding of nutrient input, retention, and losses from Rocky Mountain wetlands. Productivity is more difficult to generalize because of the great diversity of Rocky Mountain wetland types and associated plant communities.

4.2 HYDROLOGY

Wetland production, food-web relationships, and effects on downstream systems are significantly influenced by regional climate and watershed hydrologic characteristics (Livingston and Loucks 1979). Seasonal atmospheric water input and watershed characteristics regulate wetland water balances as well as nutrient loading. This section describes water input to Rocky Mountain wetlands, and possible wetland characteristics that may influence downstream flow through temporary water retention.

Water Transport to Wetlands

Wetlands receive water via surface runoff, groundwater flow, and direct precipitation. The relative importance of each mode of water input varies between wetlands.

Surface runoff and soil drainage. Rates and percentage of precipitation that enter wetlands from surface runoff are functions of watershed topography, soil characteristics, vegetation cover, and water table. Certainly stream flow is greatly facilitated by the steep vertical gradients characteristic of much of the Rocky Mountains.

[1]Authored by C. F. Knud-Hansen.

Rocky Mountain wetland soils typically have poor drainage properties. Some alpine soils are not well developed due to low soil moisture, cold temperatures, steep terrain, and the hard granite bedrock (Retzer 1956). Subalpine and Montane soils from the Colorado Front Range are sandy loam (Marr 1967). Lower-elevation soils are generally deeper and more permeable, except in areas of glacial scouring (Leaf 1975b). Denser humic gley soils, however, may develop in montane meadow regions, which permits very little vertical drainage (Western Land Grant Universities 1964).

Permafrost, found in some Alpine and Subalpine regions under wet soils, also affects soil's capacity to drain (Owens 1980). Insulated by snow, frozen soils often have greater runoff compared to thawed soils (Despain 1973).

The effect vegetation has on surface runoff and soil moisture retention is well documented (e.g., Likens and Bormann 1974). Briefly, vegetation reduces surface flow by physical obstruction, by reducing velocity of impact of rain, by increasing soil depth, and by increasing water loss through evapotranspiration. Removal of surface vegetation increases water loss from surface flow.

Groundwater flow. Groundwater flow into freshwater wetlands has been poorly studied. In the Rocky Mountains, peak groundwater flow, a comparatively minor source of water, may coincide with peak surface flow. An exception is where seeps and springs surface and give rise to wetland systems (Leaf 1975b).

Depth to water table reflects the capacity for vertical drainage of a given area. With less drainage to groundwater there will be a greater proportion of surface runoff. In Subalpine regions, ponded water is rare, and the water table is essentially nonexistent (Wilson 1969). Thin soils are saturated in the spring, but can lose up to 85% of their moisture by late fall (Ellison 1954). Seepage slopes are common (Wilson 1969) and can result in solifluction, where wet soils slowly (1-2 cm/yr) flow down slope to form terraces, which can eventually become established wetlands (Benedict 1970).

Montane soils have fluctuating water tables, but rarely exhibit seepage slopes (Wilson 1969). Wilson also noted that because of higher precipitation and gentler vertical gradients, western slope valleys in Rocky Mountain National Park had more sluggish drainage and therefore more areas with high water tables. Rooted vegetation also significantly affects depth to water table, through evapotranspiration, as demonstrated by the ability of spruce and aspen trees to remove soil moisture down to eight feet (Leaf 1975a).

Direct precipitation. Direct precipitation is probably the least significant source of water to Rocky Mountain wetlands because of the reported absence of ombrotrophic bogs. In a Minnesota minerotrophic bog (i.e., fen), Gorham and Hofstetter (1971) demonstrated, through pore water tritium measurements, that most direct rainfall is either rapidly evapotranspired (Verry and Boelter 1979) or drains laterally off the bog. Peatland, already saturated with water, does not retain additional water from rainfall. In an English bog, 50% of precipitation left via stream flow (Crisp 1966). In terrain depressions where snow has accumulated, however, direct precipitation can be considered a significant source of water for wet areas created beneath melting snow (Leaf 1975b; Willard 1979).

Water Storage and Movement Through Wetlands

There are several hydrologic parameters that should be kept in mind when discussing water storage and movement through wetlands. Important factors include the following: (1) water velocity, which affects turbulence and sediment load; (2) renewal rate, which refers to the rate of water replacement within wetlands; and (3) timing, or the regularity/predictability of daily and seasonal water input (Gosselink and Turner 1978).

Riparian wetlands. Riparian wetlands receive most of their water via surface runoff during late spring-early summer snowmelt. Because alluvial soils are more mineral in nature, water-holding capacity is relatively poor, and drainage is rapid (Bierly 1972). Wider floodplains and the physical resistance of shrubs and trees reduce stream velocity.

When stream velocity is sufficiently reduced, accumulation of organic matter from decomposing plant material occurs. Hydric soils may develop, permitting greater water retention (Foth and Turk 1972), initiating a transition between a riparian wetlands to a marsh wetland. This evolutionary scenario may require thousands of years to complete (Foth and Turk 1972).

Marshes. As previously suggested, marshes contain deeper soils with a greater organic content than riparian wetlands. But whether marshes were created on stream floodplains or from soil deposition in natural depressions, the inorganic generally exceeds the organic fraction (Ellison 1954). Nevertheless, a higher soil organic content and resultant increase in pore space enable alpine (subalpine) wet meadows to slow snowmelt runoff, reducing flood risk and soil erosion (Owens 1980). Water retention effectiveness is in great part due to the extent of detrital accumulation and degree of natural channeling within the marsh. More extensive channelizing can increase detrital export and reduce the soil moisture retention capabilities.

Fens and bogs. Fens and bogs, found in cool climates where water input exceeds evapotranspiration (Verry and Boelter 1979), are characterized by peat accumulation up to several meters deep. Most water entering peatlands leaves as vapor from evapotranspiration. The remainder leaves by surface runoff and recharged groundwater, or it is stored in the peat (Verry and Boelter 1979).

Peat composition greatly affects horizontal and vertical water movement and water retention. High organic content from partially decomposed plant material gives all peats at least 80% pore space (Verry and Boelter 1979). Surface peats have higher fiber content and conduct water more readily than deeper peats consisting of more finely broken-down organic matter (Bay 1969; Boelter 1970). This vertical stratification from coarse fibrous peat to deeper, more dense peat has been demonstrated in cores taken from a Minnesota bog (Gorham and Hofstetter 1971) and four fens in the Colorado Front Range (Pennak 1963). At Elk Creek Bog in Wyoming's Medicine Bow Range, Sturges (1967, 1968) reported bulk densities of 0.160 g/cm^3 and 0.216 g/cm^3, and hydraulic conductivities of 23.9 x 10^3 cm/day and 16.1 x 10^3 cm/day for peat samples collected at 46 cm (18.1 in) and 91 cm (35.9 in). Again, surface peat samples released

water more readily than deeper samples. Water movement in surface peat can be as much as a thousand times greater than water movement in deeper parts of the bog (Verry and Boelter 1979).

The ability of a peatland to retard or reduce downstream peak flow is a function of the water table in the peat profile, hydraulic conductivity of the peat, and slope of the system. In the spring, with high runoff, low evapotranspiration, and high water tables, topography controls runoff characteristics through a peatland more than the hydraulic properties of the peat itself (Bay 1969; Gorham and Hofstetter 1971). Fens and bogs will yield the most water at this time and, because of high water tables, will tend to channel the water through. During the summer, intermittent water input and high evapotranspiration rates (Verry and Boelter 1979) lower the water table, permitting groundwater recharge. Under these conditions, four Minnesota bogs were unable to sustain downstream summer flows, but were able to delay by 1-9 hours storm peak runoff (Bay 1969). Peak flow from storm runoff through an Alaskan Sphagnum moss bog had lag times up to 21 hours (Dingman 1966). Verry and Boelter (1979) suggested that if a Wisconsin watershed were about 30% wetland, peak flow could be reduced 60%-80%.

An additional factor influencing a peatland's capacity to store water is the potential for vertical water movement. Surface water percolation down through a fen or bog is affected by peat accumulation and decomposition (Gosselink and Turner 1978). Tritium measurements in a Minnesota bog core indicated downward water movement was impeded by a bottom layer of very dense, well-decomposed peat (Gorham and Hofstetter 1971). Pennak (1963) also observed a dense stratum of bluish grey clay (gley) beneath the more fibrous peat in four Colorado fens. This suggests that net water movement in many fens and bogs is horizontal.

Table 31 summarizes major mechanisms of water input, output, and flow through several types of wetland systems. Raised convex bogs (ombrotrophic) and tidal marshes do not exist in the Rocky Mountains, but are included for comparison with other wetland types. Figure 69 relates topography, substrate, aspect, and elevation to soil moisture. This figure is particularly useful in understanding factors influencing Rocky Mountain hydrology.

4.3 NUTRIENT CYCLING IN WETLANDS

Nutrients are organic and inorganic constituents utilized for plant and animal growth. The rate of nutrient input, storage, and release influences wetland floristics, vegetation types, productivity, decomposition, peat accumulation, and system evolution (Heinselman 1963). Figure 70 illustrates the basic nutrient pathways and transformations characteristic of freshwater wetlands (Heliotis and DeWitt 1983). Investigations of nutrient dynamics in cold-climate, freshwater wetlands are few, and tend to focus on one or two mechanisms. Variations in time of year, methodologies, and site hydrology make generalized conclusions concerning nutrient transport/retention based on mass balance computations impossible (Kadlec 1979).

Table 31. The major hydrodynamic characteristics of different wetland types. (From Gosselink and Turner 1978.)

	Water inputs to marsh				Type of water flow				Outputs from marsh			
Marsh type	Capillary	Precipitation	Upstream	Downstream	Capillary	Subsurface	Surface sheet flow	Overbank flooding	Percolation	Evapotranspiration	Downstream runoff	Hydro-pulse
Raised-convex	+	+			+	+			+	+		Seasonal
Meadow	+	+	very little (+)			+			+	+	very little	Seasonal
Sunken-convex		+	+			+	very slow			+		Seasonal
Lotic		+	+			+	+	+		+	+	Seasonal
Tidal		+	+	+		+	+	+		+	+	Tidal
Lentic		+	+			+	+	+		+	+	Variable/ seasonal

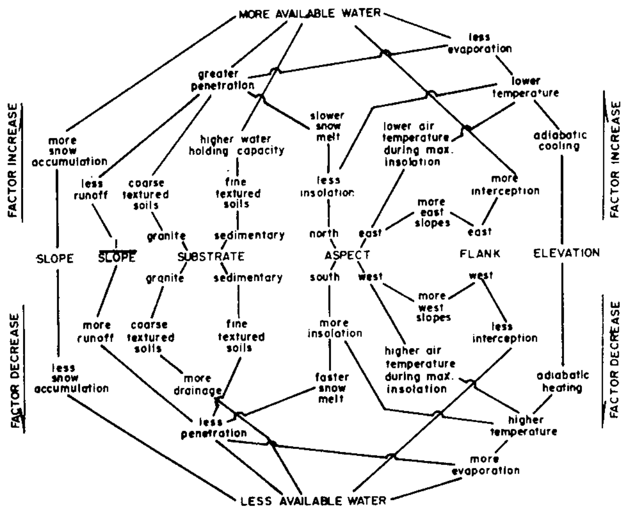


Figure 69. Diagrammatic representation of relationships of some factors producing the moisture regime of a habitat. (From Despain 1973.)

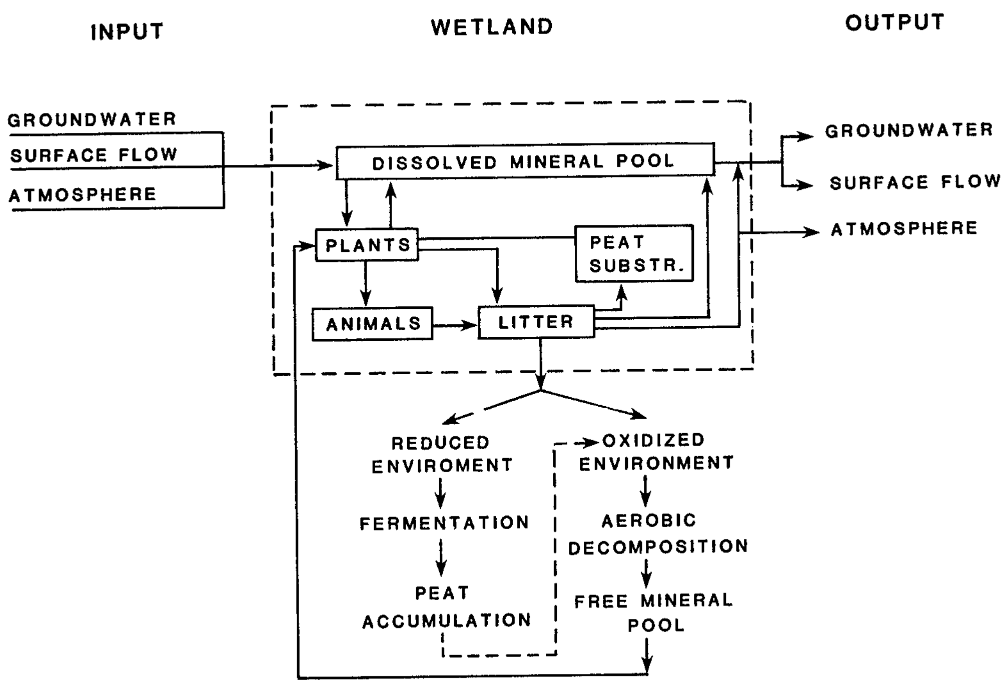


Figure 70. A simplified model of nutrient cycling in a freshwater wetland system. (After Heliotis and DeWitt 1983.)

Nutrient Sources

Stream water. Stream water contributes the majority of nutrients to most freshwater wetland systems other than ombrotrophic bogs. Three factors influencing this nutrient input are stream flow or discharge, watershed bedrock and soil characteristics, and nature of the upstream plant community.

High-elevation Colorado streams have a pH of around 7.0, and tend to be nutrient poor. Representative concentrations reported by Leaf (1975a) include 0.8 - 1.0 mg/ℓ nitrate (NO_3^{1-}), 1.8 - 14.5 mg/ℓ calcium (Ca^{2+}), 0.8 mg/ℓ magnesium (Mg^{2+}), 10.0 - 14.6 mg/ℓ sulphate (SO_4^{2-}), and <0.01 mg/ℓ phosphate (PO_4^{3-}). Nutrient concentrations are related to flow, with greater concentrations correlating with lower stream discharge (Bond 1979). In an investigation of Como Creek, Colorado, Lewis and Grant (1979a) revealed a more variable effect with flow. Bicarbonate (HCO_3^-), NO_3^-, Ca^{2+}, Mg^{2+} and sodium (Na^+) concentrations decreased with increased discharge. Ammonia (NH_4^+), dissolved organic phosphrous and nitrogen, potassium (K^+) and SO_4^{2-} exhibited no trend; dissolved organic carbon (DOC), hydrogen ion, and PO_4^{3-} concentrations increased with stream flow. For all elements, however, loading (concentrations x discharge) increased with increasing stream discharge. Increased stream flow also increases suspended sediment concentrations and losses from montane watersheds (Leaf 1975a). Deep upstream snowpacks increase runoff discharge and maintain cold soil temperatures and soil frost. Watershed nutrient transformations, such as bacterial ammonia production and oxidation to nitrate, are accelerated with warmer temperatures. Increases in biological activity and nitrate losses can be three times greater with a shallower versus a deeper snowpack (Lewis and Grant 1980).

Watershed bedrock and soil characteristics naturally affect stream water chemistry. Soils are derived from geologic weathering, fluvial deposition, organic accumulation (Brown et al. 1978), and silts and clays blown in from lower elevations (Osburn 1963; Owens 1980). The thin, course soils on granite bedrock (Retzer 1956) do not release significant amounts of nutrients and tend to be acidic. Where there are limestone and shale outcroppings, soils are more finely textured, higher in nutrients, and buffered due to calcium carbonate (Bamberg and Major 1968; Despain 1973). Accumulated organic matter in high-elevation grassland sediments ranges around 1%-8% (Ellison 1954; Mueggler and Harris 1969), and up to 59% on the surface of some Colorado subalpine and alpine soils (Chapin 1981). Chapin reported very low phosphorus concentrations of 3 - 12 μug/cm³ for these soils. For a detailed description of Rocky Mountain soils, see Johnson and Cline (1965).

Watershed vegetation characteristics greatly influence the organic carbon and dissolved mineral loading in stream water. Nearly 60% of the total organic carbon in subalpine Findley Lake (Washington) was derived from upland snow,

fluvial, and litterfall sources (Wissmar et al. 1977). In the Rockies, particulate organic carbon (POC) transport is less above treeline and in the subalpine, where small aspen stands represent the primary broadleaf tree type (Marr 1967). Daubenmire (1974) found quantitative chemical differences in leaf litter from 12 Rocky Mountain tree species. Populus tremuloides leaves were greatest in percent N and K^+, and second to Larix occidentalis in percent P and Abies grandis in percent Ca^{2+}. Along montane streams, cottonwood, willow, alder, and birch are common (Marr 1967), with seasonal leaf litter fall contributing particulate and dissolved organic carbon to streams and riparian wetlands. Dissolved organic carbon (DOC) concentrations range from 1-4 mg/l in Colorado mountain streams (Caine 1982). The DOC originates primarily from living and dead plant material that leaches into snow and rain water (Thurman 1985) and dissolved peat from upstream wetlands (Caine 1982).

Groundwater. Groundwater can be a significant source of nutrients to spring-fed (Sturges 1967) and groundwater (Verry 1975) fens. Sturges (1967) found that in Elk Creek Bog, Wyoming, cation concentrations in groundwater increased during September when the water table was low, and decreased back to spring levels in October with recharge. A Minnesota fen had increased cation (Ca^{2+}, Mg^{2+}, Na^+, K^+) and trace metal (copper, zinc, manganese) input due to groundwater dissolution of bedrock (Verry 1975). Sarnecki (1983) also reported trace metal input to a Colorado Front Range fen via groundwater.

Atmosphere. Atmospheric input of nutrients can be a significant component of wetlands, although absolute loading rates may be small. This is particularly true with ombrotrophic bogs, which do not receive any stream-water borne nutrients (Gosselink and Turner 1978).

The principal source of oxygen for many wetlands is from direct diffusion from the atmosphere (Sparling 1966). This becomes a less important source as depth of standing water increases, where the proportion of oxygen derived from photosynthetically active attached and planktonic algae and submerged higher aquatic plants increases.

Rainwater can be an important source of nitrogen as dissolved N_2, NO_3^-, and NH_4^+. Most atmospheric nitrogen originates from ammonia released from decomposing terrestrial vegetation (Wetzel 1983). The ammonia adsorbs readily to inorganic particles or can be oxidized to nitrate. Because of ammonia's adsorptive properties, snow often contains more nitrogen than rainwater; dry fallout can contain 10 times more nitrogen than wet precipitation (Wetzel 1983).

Urban activity can greatly affect atmospheric nutrient input. Phosphorus loading is mainly from dust returned to Earth as dry fallout or washed out of the atmosphere with precipitation. Increased soil erosion from agriculture, together with industrial activity, can significantly raise atmospheric ammonia,

phosphorus, and sulfate concentrations (Likens et al. 1972; Grant and Lewis 1982; Wetzel 1983; Oppenheimer et al. 1985). Elevated sulfur concentrations in the intermountain airshed of the Rocky Mountains results from SO_2 emissions transported up to 1,000 km (1,609 mi) from western nonferrous smelters and electric power plants (Oppenheimer et al. 1985). Precipitation chemistry in the Utah mountains varies with storm direction. Storms from the Pacific Northwest carry rainwater high in Ca^{2+}, Mg^{2+}, and Na^{+}, due to salt picked up from the Great Salt Lake. Storms originating from the Southwest cross industrial areas before reaching the mountains and contain more acidic rainwater, high in NO_3^- and SO_4^{2-} (Johnston 1984).

Biological: nitrogen fixation. Atmospheric nitrogen can be incorporated into wetland biomass through nitrogen fixation. Certain wetland vascular plant groups such as *Alnus* spp., *Dryas* spp., *Juncus* spp., and leguminous plants host nitrogen-fixing bacteria (Adamus 1983). Nitrogen fixation in *Alnus rigosa* nodules added considerable nitrogen to the downstream Lake Agassiz fen in Minnesota (Watt and Heinselman 1976). The alder, *Alnus tenufolia* is found along stream banks in Rocky Mountain montane regions (Marr 1967) and may represent a significant source of nitrogen for downstream wetlands. Many leguminous herbs grow in wetlands and adjoining uplands and must contribute NO_3^- (Harrington 1954; Weber 1976). Certain bluegreen algal species also fix nitrogen, and rates up to 9.4 g N/ m^2/hr have been reported for species associated with the mosses *Sphagnum* spp. and *Drepanocladus* spp. in Swedish wetlands (Bazsilier et al. 1978). The relative nitrogen contribution from nitrogen fixation varies considerably among wetlands (Moore and Bellamy 1974; Adamus 1983); however, in the Rockies, nitrogen fixation should be greater at lower elevations where more extensive *Alnus* spp. stands exist and the growing season is longer. Additionally, Shulls (1982) suggests the importance of nitrogen fixed abiotically by lightning and air ionization. This may represent a significant nitrogen source in the Rocky Mountains, where thunderstorms are frequent during summer months.

Biological: animal input. Migrating waterfowl represent the primary animal group (other than man) to import nutrients to wetlands (Odum et al. 1984). Franklin's gulls (*Larus pipixcan*), feeding on marsh insects, earthworms, and grain from nearby grasslands contributed, through excretion, up to 36% of annual phosphorus loading to a cattail marsh in Minnesota (McColl and Burger 1975). Wintergreen Lake in Michigan remains hyper-eutrophic partly due to annual 3- to 10-day rest stops by migrating Canada geese (*Branta canadensis*) (Manny et al. 1975). They reported that goose droppings containing 4.38% dry N and 1.34% dry P resulted in additional nutrient loadings to Wintergreen Lake of 1.29 g N/ m^3/yr and 0.39 g P/m^2/yr. The relative importance of nutrient input to Rocky Mountain wetlands by waterfowl is unknown. In high subalpine wetlands, however, nutrient loading from other natural sources may be low enough that guano from a small population of birds may be significant. Browsing ungulates and small mammals also contribute excrement to wetlands, but quantitative data are not available.

Nutrient Storage

Substrates. Wetlands store and release nutrients at different times of the year, following a general pattern of greater nutrient uptake in the spring

and release in the fall (Kibby 1978; Adamus 1983). Water quality is a function of hydrology, concentration, mass flow, and nutrient storage, all of which may change diurnally, seasonally, and historically. Wetland substrates retain various elements and compounds by adsorption to organic and inorganic particles, as precipitates chemically bound to organic matter, and as dissolved solutes in interstitial water (Kadlec and Kadlec 1979).

Three factors that strongly affect the solubility and form of many chemicals in wetlands are hydrogen ion concentrations (pH), reduction oxidation (redox) potentials, and dissolved oxygen concentrations. Precipitation unaffected by industrial and urban inputs has a pH of about 5.6 (Likens et al. 1972). Most natural stream and lake waters, however, have pH's between 6.0-8.0, due to buffering from dissolved carbonates (Wetzel 1983). High microbial respiratory CO_2 evolution from organic-rich wetland substrates (Sturges 1968) often results in subsurface pH's between 5.5-6.0. Surface bog sediments with greater hydraulic flow have higher pH's because of faster CO_2 removal (Sparling 1966). In Sphagnum bogs, carbonate buffering is lost and organic acids maintain pH between 3.0-5.0 (Verry 1975; Thurman 1985). Hemond (1980) reported that organic acids control acid-base balance in Thoreau's Bog, Massachusetts.

Organic production also affects both redox potentials and oxygen concentrations. Aerobic surface sediments are oxidizing, whereas deeper sediments, rich in organic matter are reducing. For instance, ferric iron (Fe^{3+}) is reduced to the more soluable ferrous (Fe^{2+}) form under these conditions (Wetzel 1983). Humic acid production from Sphagnum bogs also contributes to creating a reducing environment (Szilagyi 1973).

Since the presence of oxygen is critical in maintaining oxidizing conditions, depth of the oxidized layer often determines the boundary separating surface oxidizing sediments from deeper reducing conditions. Oxygen diffusion from plant roots increases with depth of the oxic layer, which is normally only a few centimeters thick (Gosselink and Turner 1978). Other factors include type of rooted vegetation, nature of rhizopheres, benthic organism activity, physical characteristics of substrate (de la Cruz 1978), and flow through the wetland (Sparling 1966). Kilham (1982) described a situation where oxygen concentration, redox potential, and pH were all directly interrelated. In a Sphagnum bog, anerobic conditions associated with high water level cause sulfate (SO_4^{2-}) reduction to form pyrite (FeS_2). A drop in water level aerates the substrate, oxidizing pyrite to H_2SO_4 (sulfuric acid), which lowers pH.

Nutrients are stored in accumulated wetland substrates in particulate form and as dissolved chemical constituents. Particulate organic matter buildup characterizes most wetlands, especially fens and bogs. In a Colorado Front Range fen, organic matter was initially deposited as a clay-algal muck during the moraine-blocked pond stage (Sarnecki 1983). Pennak (1963) found a similar substance mixed with unweathered sand and gravel beneath peat in four other Front Range fens. Peat accumulation is a function of plant production rates and duration/depth of flooding, which affects oxygen input and hence decomposition rates (Gosselink and Turner 1978). Peat depth ranges from 1-2 m (3-6 ft) in the above mentioned Rocky Mountain fens, and can reach 12 m

(3.6 ft) in some Minnesota bogs (Verry 1975). Most peatlands are thousands of years old and have very slow peat accumulation rates. Representative accumulation rates are 0.025-0.042 cm/yr or 27-52 gm/yr in a Manitoba bog (Reader and Steward 1972) and 0.019-0.045 cm/yr in Colorado Front Range fens (Pennak 1963).

Quality of organic matter changes as a wetland progresses from an algae-dominated community, to one dominated by sedges and then shrubs (Sarnecki 1983). Wetland parks in Rocky Mountain National Park have soils containing 36%-66% organic matter (Wilson 1969). Percent organic matter in Colorado Front Range fens varies from 53%-95% in surface peat, and decreases with depth down to 5%-29% just above the original stream or terrestrial substrate (Pennak 1963; Sarnecki 1983). These values are greater than most Colorado subalpine forest soils (Ellison 1954; Chapin 1981) and much greater than hydrosols found in lake bottom sediments (Boyd 1970b).

Stored nutrients adsorbed to organic substrates include phosphorus, nitrogen, and particularly heavy metals (Chapin et al. 1978; Adamus 1983; Sarnecki 1983; Richardson 1985). Generally, organically bound nitrogen from decaying vegetation represents the largest pool of nitrogen in wetlands (Kadlec 1979). Heavy metals readily adsorb to organic matter, and are often concentrated in wetland substrates. Zinc and nickel discharged from metal plating industries were found to accumulate in the sediments of a Canadian marsh (Glooschenko 1982). Sarnecki (1983) also demonstrated heavy metal accumulation in several Colorado Front Range fens (Table 32). Once incorporated in the peat, these nutrients can remain trapped from several hundred to several thousand years (Adamus 1983).

Table 32. Amounts of selected trace elements found in Front Range peats; ppm from whole dried samples. (From Sarnecki 1983.)

Locality	Cu	Mo	Ni	Pb	Th	U	Zn
Caribou Ranch, Boulder, CO	25	5	10	43	--[a]	--	47
Caribou Park, Boulder, CO	12-50	5-18	6-25	4-106[b]	5	240	25-120
Tolland, Gilpin Co.	20-81	26	17	23-60	--	--	39-120
Mammoth Creek, Gilpin Co.	11-45	3	6-20	14-37	--	--	24-110
Boston Peak, Larimer Co.	5-400[b]	0.4-36[b]	6-260[b]	6-43	1-29[b]	180-970[b]	4-420[b]

[a]-- Not detected.

[b]Notes highest concentration for corresponding element.

Inorganic particulate matter transported into wetlands by streams also contributes to wetland substrates. Watershed litterfall and stream flow help determine suspended solid characteristics, and whether a wetland will be a net source or sink of particulate matter (Kadlec and Kadlec 1979). Inorganic clays, silts, and sand transported to wetlands provide an enormous surface for adsorption of dissolved nutrients and organic matter (Kibby 1978). Phosphorus is particularly reactive, adsorbing to or precipitating with soil aluminum, iron, and calcium (Nichols 1983).

In natural systems, dominant dissolved inorganic nutrients are four cations (sodium, potassium, calcium, and magnesium) and four anions (carbonate, bicarbonate, sulphate, and chloride) (Kadlec and Kadlec 1979; Wetzel 1983). In wetlands, there is typically an imbalance, with inorganic cations exceeding inorganic anions because organic acids constitute the dominant anion (Thurman 1985). This is particularly true in colored, low pH bog water (Verry 1975).

Dissolved organic carbon (DOC) is responsible for the yellow-brown stain in wetland waters (Kibby 1978). DOC originates from surface detrital decomposition and leaching, releasing humic and fluvic acids (Verry 1975; Thurman 1985), and from very slow dissolution of peat, which also releases organic acids (Caine 1982). Thurman (1985) provided the following ranges for DOC concentrations: freshwater marshes, 5-15 mg/ℓ; swamps, 10-30 mg/ℓ; and bogs, 30-400 mg/ℓ. Ombrotrophic bogs with very little flushing represent the higher bog values. Water color is also measured by comparison with platinum-cobalt standards. Reported ranges include 75-890 units for Minnesota perched bogs (Verry 1975), over 500 units in Wyoming's Elk Creek Bog (Sturges 1967), and 60-90 units for four Colorado Front Range fens (Pennak 1963). The lower values found by Pennak could be due to more rapid flushing in the mountain fens. Ives (1942a) reported that colored water found in Colorado subalpine wetlands is locally called "swamp juice," and can be an effective organic solvent and germicide.

Wetlands also contain inorganic constituents in solution. Dissolved nitrogen is present as ammonia, nitrate, nitrite, and in organic molecules (e.g., polypeptides and amino acids). Ammonia accumulates from bacterial decomposition in anaerobic waters, or can be oxidized to nitrate in the presence of oxygen. Orthophosphate and dissolved organic phosphorus represent the two major soluble forms of phosphorus (Adamus 1983). Concentrations of these dissolved nutrients in wetlands is also greatly affected by plant uptake and decomposition rates.

Other dissolved nutrients vary in reactivity and concentration depending upon plant species, substrate type, acidity, and oxic conditions. Electrolyte concentration is a function of ionic concentrations in inflowing water and the amount added from the wetland as the water flows through (Sparling 1966). Sturges (1967) found no changes in calcium, magnesium, potassium, and iron concentrations in Elk Creek Bog water during the growing season. Cation changes would be anticipated in bogs dominated by *Sphagnum* spp. Ferric iron complexes readily with colloidal organic acids (Koenings 1976) and accumulates in interstital peat water (Sturges 1967). Anoxic reducing conditions and low pH's from humic acids lead to heavy metal enrichment in subsurface peat by complexing and adsorption (Sarnecki 1983; Szilagyi 1973). Iron and aluminum precipitates will also go back into solution faster in this reduced environment

(Verry 1975; Kadlec and Kadlec 1979), resulting in increased concentrations with depth. Furthermore, under acid conditions (pH <5.1), carbon dioxide (CO_2) represents the only form of dissolved inorganic carbon. Equilibrium reactions prevent respiratory produced CO_2 from converting to bicarbonate (HCO_3^-). The relative proportion of HCO_3^- in peat water directly relates to rate of stream flow entering the wetland; streams supply HCO_3^- and flush out CO_2 from the wetland system (Sparling 1966).

Plants. In addition to wetland substrate and interstitial water, nutrients are stored in living plant biomass. Emergents generally store more N and P than submersed or floating aquatic plants due to greater biomass per unit area (Kadlec 1979). Plants in fast-moving water also tend to accumulate more nutrients (Sparling 1966). Nevertheless, there is no reliable average composition for individual species or ecological grouping of species (Boyd 1970b,c,d, 1978). Examination of selected emergent species indicated no significant differences in cellulose, although percent nitrogen decreased with plant structural complexity (Boyd 1970c, 1978). By percent dry weight, Boyd reported values of 0.9%-2.6% N and 0.1%-0.3% P. Table 33 from Kadlec (1979) lists above-ground standing crops (g/m^2) of N and P in several vascular aquatic plants. Floating submersed species contain about half the N and P standing crops of emergents, or about 10-20 g N/m^2 and 1-2 g P/m^2 (Kadlec 1979).

Wetland plants can also concentrate heavy metals. Sarnecki (1983) found lead accumulation in rooted aquatic plants, and reported that willows and birch trees were more effective than sedges at collecting copper, molybdenum, nickel, and zinc. Cyanide used in gold and silver processing was concentrated up to 50 times in riparian aquatic plants and soils relative to concentrations in water (Noble and Howe 1983).

Nutrient Transformation

Nutrient uptake by plants. Rooted emergents take up nutrients mainly through roots, whereas submerged plants utilize both roots and foliage. Nutrients can be translocated vertically within plants via water movement and diffusion. Rooted aquatic and emergent plants tend to remove nutrients from deeper sediments and eventually deposit them on surface sediments through plant decomposition (Kadlec 1979). Thus, sediments generally act as both nutrient source and sink for emergent macrophytes. Net nutrient movement within the plant-substrate system, however, is regulated to a great extent by environmental conditions (Kadlec and Kadlec 1979; Adamus 1983).

The importance of phosphorus to freshwater wetland plant production is well documented; consequently, most experimental research has focused on factors influencing its uptake. Seasonal phosphorus mobility within an Alaskan alpine marsh dominated by *Carex aquatilis* has been investigated by Chapin and Bloom (1976) and Chapin et al. (1978). They found that soluble phosphorus available for spring plant growth came primarily from the previous fall's plant and root senescence, animal feces and urine, and lysis due to freezing of associated high bacterial populations. Autoradiographs showed high spring P uptake, with 40% of soil soluble P transferred into plants within 10 days of snowmelt. Although shoot growth continued through summer, after July there

Table 33. Above ground standing crops (g/m²) of N and P in vascular aquatic plants from selected studies reported in Kadlec (1979).

Source	Species	N	P
Klopatek (1975)	mixed emergents	16.9	3.8
Kvet (1975)	*Typha latifolia* (maximum)	25.1	1.6
Boyd (1971a)	*Typha latifolia*	5-12	0.7-1.8
Dykyjova and Hradecka (1973)	*Phragmites communis*	28-46	3.4
Ulehlova et al. (1973)	*Phragmites communis*	18.8-34.7	1.06-2.67
Boyd (1967)	*Chara* spp.	27.6	2.8
	Myriophyllum spp.	9.3	0.9
	Ceratophyllum spp.	16.7	1.3
Steward and Ornes (1975)	*Cladium jamaicense*	5.5-8.9	0.25
Boyd (1971b)	*Justicia americana* (maximum observed)	44.3	2.8
Wentz (1976)	*Carex* spp.	4-6	0.2-0.4
Brinson and Davis (1976)	*Nuphar luteum*		0.197

was a net translocation of phosphorus downward into the rhizome to be used in the following spring. This rhizome-stored P represented over 40% of the annual P requirement.

Several factors may affect phosphorus uptake rates. Phosphorus availability, and not soil temperatures even down to 1 °C, apparently regulated P uptake in an Alaskan marsh (Chapin and Bloom 1976) and in a Colorado Rocky Mountain marsh dominated by *Carex aquatilis* (Chapin 1981). The greater the soil phosphorus deficiency, the faster the uptake rate. Another factor is the plant root microenvironment, which is oxygenated by oxygen released from the roots. Soluble phosphate readily adsorbs to ferric iron precipitated onto the

root hairs and becomes unavailable to the plant (Black 1968). Koenings (1976) suggested that colloidal organics reduce iron-phosphate complexes, but that phosphate also complexes with colloidal organics, reducing P availability for plant growth. Consequently, the dissolved inorganic phosphorus (DIP) pool is small. During the growing season in an Alaskan alpine marsh, average DIP resident time was about 10 hours (Chapin et al. 1978).

Nitrogen availability also increases in spring from decomposition processes. Soil warming increases microbial activity, which increases ammonia production (Chapin and Bloom 1976). Ammonia is bacterially oxidized to nitrate and in that form used by plants (Kibby 1978). Potassium is another mobile plant nutrient that is rapidly taken from wetland soils in the spring and returned during fall plant senesence and decomposition (Breckenridge et al. 1983).

Wetland plant species may also take up and concentrate heavy metals (Sarnecki 1983; Noble and Howe 1983). These metals are incorporated into plant leaves, roots, and stems and become further concentrated in animal tissue when plants are consumed by herbivores. This concentration of trace elements up the food chain (biomagnification) is often detrimental or lethal to secondary consumers (Kibby 1978; Kadlec and Kadlec 1979). Not all micronutrients are concentrated in plants, however. Small (1972) did not find excess manganese or aluminum accumulation despite high levels in two Canadian bogs.

Sphagnum spp.-dominated bogs are a special case regarding nutrient dynamics in wetland plants. These plants exchange Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, and other cations from rain and groundwater for H^{+}. Figure 71 illustrates cation exchange processes and other chemical reactions in _Sphagnum_ bogs, including those affecting acid-base balance. This exchange reduces cation concentrations, ionic strength, and pH in bog water (Szilagyi 1973; Thurman 1985). The H^{+} is released from polygalacturonic acid (PGA), which represents up to 21.5% _Sphagnum_ dry weight. This cation exchange and the buffering capabilities of PGA can be adversely affected by outside H^{+} input from acid precipitation (pH <5.7) (Kilham 1982).

Decomposition. Decomposition of wetland plant species contributes a significant proportion of phosphorus (Boyd 1970a; Chapin et al. 1978; Nichols 1983) and nitrogen (Kibby 1976; Chapin and Bloom 1978) necessary for plant growth the following spring. Decomposition consists of three simultaneous processes: (1) rapid leaching of soluble substances; (2) weathering and mechanical fragmentation by wind, ice, animals, and incomplete grazing; and (3) oxidative and anaerobic biological decay by bacteria and fungi (Latter and Cragg 1967; de la Cruz 1978).

Several environmental factors influence decomposition rates in wetlands. Peat decomposition is strongly related to water content and hydraulic conductivity (Verry 1975; Gosselink and Turner 1978), oxygen content, pH, and temperature (Adamus 1983). Boyd (1970a) reported faster decomposition of _Typha latifolia_ in water than air, although other factors may have been of greater importance (de la Cruz 1978). Anoxia and low pH from organic acids

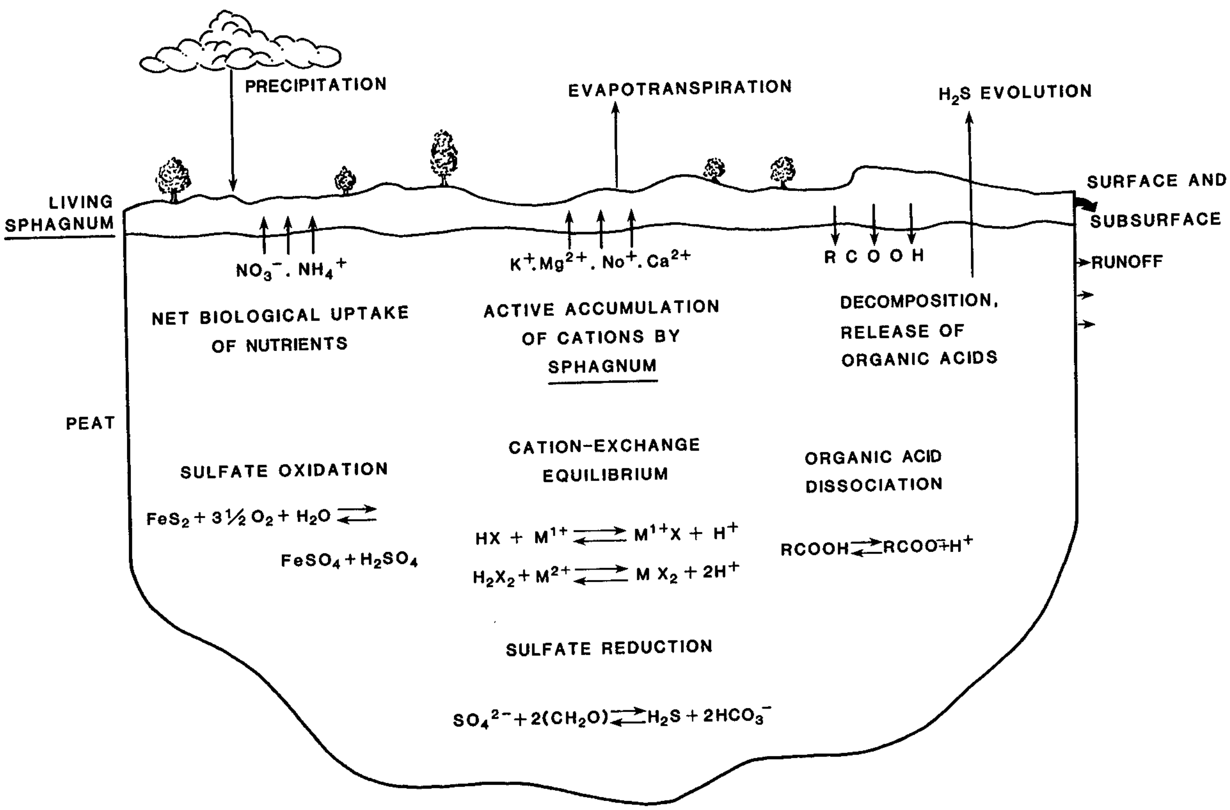


Figure 71. Schematic representation of a bog ecosystem including major inputs, outputs, and chemical reactions occurring within the system that affect the acid-base balance. (Adapted from Kilham 1982, after Hemond 1980.)

greatly retard microbial decomposition activity (Adamus 1983; Thurman 1985). Acidic environments generally favor fungal decomposition somewhat, but inhibit bacterial metabolism (Heal et al. 1981; Shulls 1982). Such conditions exist only a few centimeters from the surface in many wetlands with low hydraulic conductivity (de la Cruz 1978). Temperature is also important, and since many Rocky Mountain wetlands are frozen or snow covered soon after plant senescence, bacterial decomposition occurs primarily during spring. In some Alaskan marshes, however, Chapin et al. (1978) demonstrated that microbial growth, and not respiration, was affected by low temperatures. Therefore, the relative lack of bacteria, not inhibition of respiratory activity, was responsible for low fall decomposition rates. Warm spring temperatures permitted rapid bacterial reproduction, increasing metabolism of dead plant biomass from the previous summer.

The nature of the plant material itself influences its decomposition rate. Both high leaf nitrogen (Marinucci et al. 1983) and phosphorus (Day 1982) apparently facilitate decomposition. Lignins, found in greater concentrations in terrestrial plants for structural support, retard decomposition rate (Meentemeyer 1978; Figure 72 from Heal et al. 1981) due to interference with the enzymatic degradation of cellulose, other carbohydrates, and proteins (Melliolo et al. 1982).

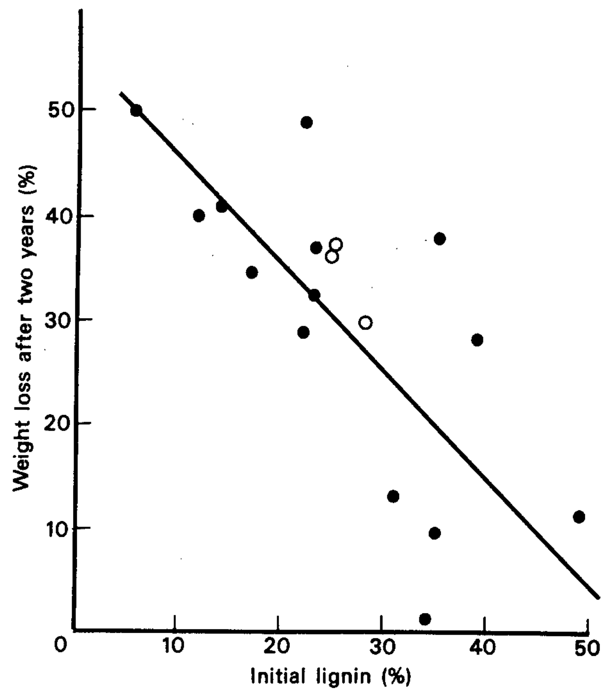


Figure 72. The relationship between percentage weight loss of litter after 2 years and the initial lignin concentration for litter at Point Barrow and Eagle Summit, Alaska (•), and Moor House, UK (o), (y=55.9-1.03x). (From Heal et al. 1981.)

Most wetland plant decomposition investigations have taken place either in estuarine water or in freshwater marshes of warmer climates. The few colder climate studies do not provide any information that can be generalized. Values for percent dry weight of above-ground plant biomass remaining after 1 year after senescence range from 70%-80% for Juncus squarrosus in an English moor (Latter and Cragg 1967), 49%-79% for a Manitoba bog (Reader and Steward 1972), and 19% for a marsh in southern Quebec dominated by Carex and Typha spp. (Auclair et al. 1976). Decomposition rates for below ground plant biomass are essentially uninvestigated.

Table 34 summarizes nutrient cycling in four wetland plant groups (Kelly et al. 1985). Shrubs, wet meadows (e.g., marshes and fens), and emergent and submergent macrophytes all store large quantities of nutrients taken up from soil and soil water. A major difference is the relatively high proportion of nutrients stored in wet meadow leaf litter, compared to litter from other plant groups.

Table 34. Nutrient cycling characteristics of marsh vegetation. (From Kelly et al. 1985.)

Vegetation zone	Source of nutrients	Nutrient storage in shoots	Fate of released nutrients	Nutrient storage in litter
shrub	soil/soil water	large; in perennial woody tissue; moderate in annual tissue	soil/soil water	moderate-high
wet meadow	soil/soil water	large; in annual tissue	soil/soil water	high
emergent	soil/soil water; surface water	large; in annual tissue	surface water; soil/soil water	low
submergent	surface water; soil/soil water	large; in annual tissue	surface water; soil/soil water	low

Nutrient Losses

Nutrient flushing. Wetlands can be net sources or sinks for organic matter (Whigham and Bayley 1979), nitrogen, and phosphorus (Kadlec and Kadlec 1979; Adamus 1983). Upon plant death, nutrients may be either incorporated into sediments or flushed out. The fate of a particular molecule depends both on its affinity for binding and the hydrodynamic characteristics of the wetland substrate.

Phosphorus retention/storage is primarily a function of soil adsorption, particularly the inorganic mineral fraction (Whigham and Bayley 1979; Richardson 1985). Wetlands remove P from inflowing water through adsorption and precipitation reactions with soil Al, Fe, and Ca (Nichols 1983). In an analysis of 20 eastern U.S. swamps and bogs, Richardson (1985) determined that P retention capacity is most directly related to extractable aluminum concentrations ($r=0.929$), and to lesser degrees iron ($r=0.621$), then pH, calcium, and organic matter. Generally, fluvial soils consisting of silt and loam rich in amorphous aluminum retain phosphorus better than peatland, but with high phosphorous loading, wetlands of any type become net phosphorus exporters.

Riparian wetlands, especially those with frequent flushing and organic substrates, accumulate the least amount of phosphorus or nitrogen (Whigham and Bayley 1979), although, nutrient retention is increased where inflow velocity is reduced and sedimentation occurs. Significant nutrient losses occur during early spring and summer from washout of dead plants from the previous year. Nevertheless, riparian wetlands tend to accumulate nutrients in the spring and release them with plant senesence in the fall (Kibby 1978). At the other hydrological extreme, raised ombrotrophic bogs tend to close the nutrient cycle and have very little nutrient flux across bog boundaries (Gosselink and Turner 1978).

In addition to losses of soluble nutrients, particulate peat erosion also occurs. An English blanket bog lost 1120 kg dry wt/ha/yr (0.8 mm/yr) from stream erosion over 10% to 20% of the bog's surface. This quantity represented losses of 20.01 kg Na/ha/yr, 7.97 kg K/ha/yr, 49.68 kg Ca/ha/yr, 0.17-0.40 kg P/ha/yr, and 9.48 kg N/ha/yr (Crisp 1966). Billings and Mooney (1959) reported mature peat hummock erosion from fens located in the Medicine Bow Range, Wyoming. In this case, wind-blown ice particles were the agent.

Gases. Nutrient export through wetland gas production is common in most wetlands. Losses of methane, carbon dioxide, and hydrogen sulphide may occur (de la Cruz 1978). Methane and hydrogen sulphide are produced anaerobically and may be trapped by the surface oxidizing layer (Kibby 1978). Methane, however, represented nearly 45% of total carbon losses from water-logged organic soils in a Swedish mine (Heal et al. 1981). The major nutrient loss is nitrogen through denitrification, the bacterially mediated conversion of nitrate to nitrogen gas. There is greater denitrification in wetlands than terrestrial systems due to high organic loading and the near-surface oxic/anoxic microzone (Kadlec and Kadlec 1979; Adamus 1983). Nitrate in the oxic surface water is reduced to N_2 at the oxic/anoxic interface by bacteria requiring organic substrates as their carbon source. Denitrification rates are strongly temperature dependent and are zero under freezing conditions, causing an increase in soil nitrate concentrations (McGarity 1962; Nichols 1983). Because of the difficulty of measuring and the seasonal variability of denitrification, accurate nitrogen loss estimates and hence wetland nitrogen balances are impossible to calculate (Kibby 1978).

Biological transport. The last mechanism of nutrient export from wetlands is through biological transport. Most Rocky Mountain wetlands are grazed by waterfowl, beaver (*Castor canadensis*), moose (*Alces americana*), muledeer (*Odocoileus hemionus*), and elk (*Cervus canadensis*). High subalpine wetlands also may be grazed by bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*) in summer and fall. Depending on where they defecate, however, these herbivores may better represent nutrient processors rather than nutrient exporters (Heliotis and DeWitt 1983). The same may be said for cattle and sheep grazing, which can have even a greater impact. Small, transient populations of waterfowl are probably the dominant biological exporters of nutrients (Odum et al. 1984).

4.4 PRODUCTIVITY

Primary Production

Primary production refers to the biochemical conversion of light energy to chemical bond energy through photosynthetic production of reduced organic molecules. In wetlands, this process is conducted by algae and lichens; mosses and liverworts; ferns and horsetails; submerged and emergent macrophytes; woody plants such as Salix spp., Alder spp., Populus spp., and Picea spp.; herbs; and graminoids. The rate at which biomass (primary production) is accumulated is primary productivity (Wetzel 1983).

Factors regulating primary productivity. Those factors influencing wetland primary production rates can be grouped into three categories: climatic conditions, nutrient availability, and water availability.

a. Climatic conditions. Temperature is the most studied climatic variable in northern and high altitude freshwater wetlands. Not surprisingly, natural selection has resulted in plants well adapted for these cold environments, even down to 0 °C (Bliss 1966; Owens 1980). Although there is less plant species diversity in areas with extreme soil frost or snow accumulation (Heifner 1974), peat fracturing due to freeze/thaw cycles (Fahey 1971) produces different soil characteristics and may support different plant types (Billings and Mooney 1959). Chapin (1981) found plant species stratification based on temperature in Alaskan and Rocky Mountain (Colorado Front Range) subalpine wetlands. He reported wetlands dominated by Carex aquatilis on the coolest soils, Scirpus spp. on moderate soil temperatures, and Eleocharis palustris and Typha latifolia on the warmest soils.

Although certain plant species are adapted to cold climates (e.g., P uptake, Chapin and Bloom 1976), lower soil temperatures reduce growth rates. The inverse relationship between Carex aquatilis tiller height and temperature is one such example (Chapin 1981). In another study of 11 pure Carex spp. stands, Gorham (1975) found a significant correlation ($r=0.84$) between highest monthly mean temperature and above ground standing crop (Figure 73). This relationship was expressed as $C=0.057(t)+1.80$, where $C=\log_{10}$ terminal crop (g dry wt/m²) and t = highest monthly mean temperature (°C). Root respiration, however, was greater in Alpine versus Subalpine plants in the northern Rockies (Higgins and Spomer 1976). The authors suggested that this gave the Alpine species a competitive advantage over invading species from lower elevations.

One factor influencing soil temperature in spring is the depth of snowpack. Carex spp. shoots are capable of emerging through snow and ice (Gorham and Somers 1973). Nevertheless, deep snowpacks lasting into the summer essentially shorten the growing season and thus reduce primary productivity (Billings and Bliss 1959; Ostler et al. 1982).

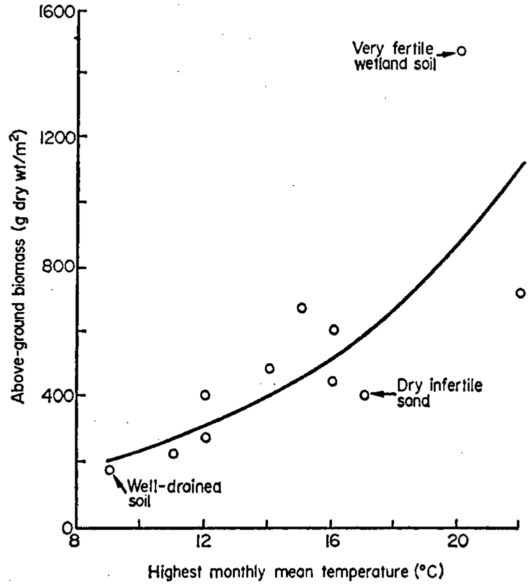


Figure 73. Relationship between above-ground standing crop of various sedges and the highest mean monthly temperature near the site. Sites are wetlands except where noted otherwise. (From Gorham 1975.)

Two other climatic variables are light and wind. Insufficient light energy for photosynthesis has not been reported in wetlands; in fact, Bliss (1966) reported that Carex spp. and Juncus spp. dominating wet meadows on Mount Washington's Alpine Zone utilize solar energy very efficiently. A different situation exists in Montane regions where canopy cover may significantly shade smaller wetland plant species below. Wind affects plant distribution and productivity indirectly by accumulating soils in Subalpine depressions allowing certain species to grow (Ellison 1954; Osborn 1963, 1969), and by seed and propagule dispersal. Direct effects of wind on plants include increasing evapotranspiration, wind stress, and burial by drifting snow (Forrest 1971). Wind stress in the Rocky Mountains is greater in the Alpine and Subalpine Zones relative to the Montane due to greater wind force and reduced protective terrestrial vegetation (Marr 1967).

b. Nutrient availability. Nutrient availability plays a significant role in regulating wetland primary productivity. Rates of nutrient input, cycling, and export from wetlands help regulate plant production (Kadlec 1979). Phosphorus is apparently the nutrient in least supply relative to demand in most cold-climate freshwater wetlands. Evidence suggests phosphorus limitation in Finnish peat soils (Paavilainen 1974), Alaskan wet meadows (Barel and Barsdate 1978), a Canadian wet meadow (Auclair et al. 1976), and an English bog (Loach 1968). Gore (1961), however, found no P limitation in another English blanket bog. Interspecific competition, rapid microbial phosphorus uptake (Richardson 1985), low inorganic soluble phosphorus concentrations, and factors restricting phosphorus uptake all contribute to phosphorus limitation.

Other nutrients with lesser stimulatory effects on wetland plant production include nitrogen in some Sphagnum spp. bogs (Paavilainen 1974), potassium (Loach 1968; Paavilainen 1974), and extractable calcium (Auclair et al. 1976). There was not a good relationship between total dissolved solids concentration and plant composition in some Swedish bogs and fens (Sjors 1950). In fact, high salt concentrations are often detrimental to freshwater macrophytes (Gooselink and Turner 1978). High cation loading can be lethal to Sphagnum, which grows better in nutrient-poor ombrotrophic bogs (Kilham 1982).

It is impossible to generalize nutrient limitation in Rocky Mountain wetlands. The supply of phosphorus limits aquatic productivity in most temperate regions; yet data from mountain lake systems suggest nitrogen may be the limiting nutrient. Montane California Lakes Tahoe and Castle have demonstrated nitrogen limitation (C.R. Goldman, pers. comm.). Morris (1985) showed nitrogen limitation in several Rocky Mountain Montane lakes. And the observation of free-living nitrogen fixers in the Colorado Alpine Zone also suggests nitrogen limitation (Shulls 1982).

A positive relationship exists between plant growth and distribution versus pH for many wetlands other than Sphagnum bogs (Kilham 1982). This was demonstrated in 113 peatland stands in Canada (Jeglum 1971), and in an array of Swedish bogs and fens (Sjors 1950). The relationship is probably not causal, but owing more to greater bacterial decomposition and nutrient availability in peatlands with higher pH's (Verry and Boelter 1979). More acidic waters also reduce carbonate and bicarbonate availability, which may affect peatland plant distribution (Sparling 1966). Some Rocky Mountain wetlands are alkaline, as evidenced by white precipitates along the margins (Daubenmire 1974). How productivity and nutrient processing differ in these compared to other Rocky Mountain wetlands is not understood.

c. Hydrology. Another factor influencing wetland primary production is hydrology. Water level and flow through wetlands affect nutrient loading, decomposition, and build-up of plant toxins, such as anaerobically produced hydrogen sulphide (Loach 1968). Changes in water level may affect relative dominance of emergent versus submerged plant species (Millar 1973). Bierly (1972) reported that Rocky Mountain fen and marsh vegetation strongly related to geomorphology and drainage. There was a continuum of vegetation forms along a soil moisture gradient, although species diversity decreased at the extremes of year-round water supersaturation and summer drying. Lateral plant zonation related to soil moisture (Langeheim 1962) or related to snow duration (Willard 1979) occurs both along edges of Alpine snowpatches gradually melting during the summer (Langenheim 1962), and between raised hummocks in subalpine bogs (Heifner 1974). Freezing of water into sizeable ice masses in saturated peatland produces these hummocks, which provide a mosaic of soil moistures in the bogs. Willow carr species distribution in the southern Rockies is also strongly related to soil moisture (Phillips 1977), but the effect may be more on seed germination and seedling establishment rather than adult survival (McLeod and McPherson 1973). From an investigation in Rocky Mountain National Park, Wilson (1969) concluded that Montane and Subalpine wetland plant communities vary according to water table. Transect analysis from the wettest and most flooded areas progressing to drier wetlands indicated Montane vegetation

changing from rostrato sedge communities, tufted hairgrass, bluejoint grass, to willow. In the Subalpine, plant zonation was also strongly associated with soil water levels. Marsh marigold was more adapted to higher water tables, while Subalpine daisy was found in drier soils.

Riparian wetlands tend to have relatively high productivity due to sediment deposition with flooding and a more consistent input of nutrients (Brown et al. 1978; Gosselink and Turner 1978). Walters et al. (1980) reported variable tolerance to changes in water level by Rocky Mountain riverine tree species.

Primary production rates. Wetlands generally have relatively high production rates due to lack of water stress, generally good nutrient supply, and well-adapted plants (Richardson 1979). Plant productivity estimates for cold-climate wetlands vary considerably, with higher values reaching nearly 2,000 $g/m^2/yr$ (Table 35). Reported maximum daily production rates for grass/sedge-dominated wetlands range from 0.6 - 2.3 g/m^2 (Wyoming, Billings and Bliss 1959), 2.3 g/m^2 (Swedish Lappland, Pearsall and Newbould 1957), 4-6 g/m^2 (southern Canadian Rockies, Gorham and Somers 1973), to 8 g/m^2 (Mt. Washington, New Hampshire, Bliss 1966). Although, measurements of primary productivity are rare for Rocky Mountain wetlands, Sturges (1968) estimated a value of 168 g dry $wt/m^2/yr$ for Elk Creek Bog, Wyoming. This rate is low when compared to other cold-climate wetlands (Table 35).

Most productivity investigations examine only shoot biomass and productivity; but, as Table 35 illustrates, root biomass can also represent a considerable fraction of total plant growth (Daubenmire 1941; Holch et al. 1941; Forrest 1971). Chapin and Bloom (1976), studying an Alaskan marsh, discovered that seasonal shoot growth began before root growth, but root growth continued into the fall, long after shoot senesence.

Generalizing primary productivity in Rocky Mountain wetlands is impossible due to great ranges of precipitation, mean monthly temperatures, and length of growing season found with latitude and altitude. Variations in hydrology, nutrient loading, and plant communities also may contribute to variable production rates. This is obviously one major gap in our understanding of these freshwater ecosystems.

Secondary Production

Secondary production refers to all productivity associated with all consumers feeding entirely or in part on organic material photosynthetically produced. Direct consumption of wetland algae and macrophytes is minimal, with export of paticulate and dissolved organic material probably more significant (Crow and MacDonald 1979). Secondary production rates are influenced greatly by detrital production, detrital flux to the water, and assimilation of detritus (de la Cruz 1978). Table 36 summarizes models of resource utilization and energy transfer in wetland secondary production (Crow and MacDonald 1979).

Table 35. Representative primary production values in cool-climate freshwater wetlands (data for above ground production unless otherwise noted).

Location	Wetland type	Plant type	Biomass (g/m^2)	Productivity ($g/m^2/yr$)	Ref.
Wyoming	Elk Creek Bog	spike sedge, *Carex*, marsh marigold		168	1
New York	marsh	*Carex lacustris*	1,470 226*	1,580	2
Idaho/Utah	artificial	*Phragmites communis* *Typha latifolia* *Scirpus acutus*	1,447 760 580	-- -- --	3
Minnesota	marsh	*Typha* spp. *Zizanica aquatica*	1,680 580	-- --	4
Minnesota	marsh	*Carex rostrata*	1,071	--	5
Mount Washington	meadow	*Carex* spp. *Juncus* spp.	203 81	-- --	6
N. America 42°N-45°N	5 marshes	*Carex* spp. *Carex* spp.	-- --	870±80 180±30*	7
N. America 41°N-46°N	5 marshes	*Typha* spp. *Typha* spp.	-- --	1,270±600 1,430±220*	7
N. America and England	9 bogs and fens			503±230 400±430*	7
Canada	Montane fen	*Carex rostrata* *Carex aquatilis*	650 380		8
Canada	meadow	*Carex* and *Typha* spp.	--	820	9
Canada	bog muskeg bog forest lagg	-- -- -- --	-- -- -- --	1,943 993 710 1,631	10

Table 35. (Concluded)

Location	Wetland type	Plant type	Biomass (g/m^2)	Productivity ($g/m^2/yr$)	Ref.
England	7 blanket bogs	--	--	659±53	11
England	blanket bog	<u>Sphagnum</u> spp.	100	45	12
Sweden	meadow	sedges and grasses	283	--	13

*underground plant material

References:

1. Sturges 1968
2. Bernard and MacDonald 1974
3. Breckenridge et al. 1983
4. Bray et al. 1959
5. Bernard 1973
6. Bliss 1966
7. Richardson 1979
8. Gorham and Somers 1973
9. Auclair et al. 1976
10. Reader and Stewart 1972
11. Forrest and Smith 1975
12. Forrest 1971
13. Pearsall and Newbould 1957

Table 36. Wetlands secondary productivity: summary of models of energy transfer, resource utilization patterns, and temporal utilization patterns. (From Crow and MacDonald 1979.)

Modes of energy transfer	Resource utilization patterns	Temporal utilization patterns
	TROPHIC RESOURCES:	
Direct consumption of primary producers	Direct grazing Onsite detritus utilization	Permanent wetland populations
Food web predator-prey transfer	Offsite detritus utilization Cycling of bacteria-rich detritus and fecal matter	Seasonal wetland use by local populations
Detritus export	Predator-prey interactions	
	NONTROPHIC RESOURCES:	
DOC* leachates from plants, excretion from animals	Breeding sites and nursery areas Flight staging areas	Seasonal wetland use by populations
Export of larvae and juveniles	Resting areas Refuge from predators	Occasional wetland visitors from adjacent habitats

* DOC - dissolved organic carbon.

Investigations of freshwater wetland secondary production are rare. Most research has focused on estuarine secondary production, or downstream utilization of particulate carbon. The following discussion on animal utilization of cold climate wetlands first examines permanent inhabitants, and then addresses temporary or seasonal residents.

Permanent inhabitants. Microfauna are by far the primary utilizers of primary production. Other secondary consumers, such as small vertebrates and invertebrates, often utilize only a small fraction of the plant biomass (MacLean 1981; Wetzel 1983). In an English moor, Latter and Cragg (1967) reported bacterial and fungal biomass of 28-197 g/m^2 representing up to 2/3 of total faunal biomass. In an Alaskan wet meadow, microbial biomass dominated the fauna, with peak biomass in late spring flourishing on the previous summer's plant production in the warmer spring temperature (Chapin et al. 1978).

Small invertebrates inhabiting wetlands increase substrate aeration through burrowing activity while feeding on bacteria, fungi, and detritus (Adamus 1983). Leaf litter washed into wetlands is also utilized by invertebrates (Wissmar et al. 1977). Macroinvertebrates, including insect larvae, are strongly associated with submerged vegetation. Potamogeton spp., Lemna spp., and Chara spp. harbor these organisms, with animal abundance related to leaf surface area (Rosine 1955; Krull 1970). Voigts (1976) investigated four prairie marshes in Iowa and found snails, midges, isopods, and amphipods dominating the macrofauna. Total abundance increased going inward from emergent to submerged vegetation. Figure 74 illustrates the faunal shifts associated with changes in dominant vegetation types. Erman and Erman (1975) examined seven fens in the California Sierra Nevada. Aquatic oligochaetes predominated (7.4-58 $g/m^2/yr$) and were positively correlated with peat depth due to less diel changes in temperature, oxygen, and water level in the deeper substrates. Other faunal components included ceratopogonids, chironomids, and nematodes totaling 0.05-1.0 $g/m^2/yr$. The authors noted that faunal composition and production of these seven fens were quite similar to lake benthos in oligotrophic lakes. MacLean (1981), investigating the Swedish tundra, reported invertebrate biomass 10 times greater than peak small vertebrate biomass, and 100 times greater than reindeer biomass. Invertebrates utilized only 5% of primary production on peat sites, and 30%-40% on mineral sites where earthworms dominated. Less than 10% of invertebrate production was converted to carnivore production.

Small mammals such as meadow voles (Microtus pennsylvanicus), pocket gophers (Thomomys talpoides), field mice (Peromyscus spp.), shrews (Sorex spp.), and ground squirrels (Citellus spp.) live in many Rocky Mountain wetlands that are only seasonally wet. They tunnel in the upper 46 cm (18 in), clip and eat above and below ground plant parts, and defecate, but no quantitative data are available describing these processes for the Rocky Mountain region.

Beaver and fish are the dominant, permanent vertebrate residents in many Rocky Mountain wetlands. Fish require standing water year round, and are found primarily in pools and impounded streams. Generally omnivores, fish grow quite slowly in the cold mountain pools. The beaver's impact is one of both creating wetlands and consuming selected emergent plants, such as Salix spp. and Populus spp. (Grasse 1951). An investigation by Maguire (1974) suggested that the impact of beaver on nutrient cyclying may be minor. In a Michigan peatland, beaver populations were responsible for cycling only about 1% of the nitrogen.

Seasonal inhabitants. Seasonal inhabitants of Rocky Mountain wetlands utilize these areas for both trophic and nontrophic purposes. Muledeer and elk use willow carrs for food and shelter (Heifner 1974; Phillips 1977) and meadows for grazing. Elk, when foraging in Upper Montane wetland regions of Rocky Mountain National Park, prefer Kentucky bluegrass, bluejoint reedgrass, Carex spp., and willow stems and leaves (Hobbs et al. 1981). Moose use willow carrs for shelter and fens for grazing. Mink (Mustela vison) and muskrat (Ondatra zibethica) are also found in wetlands, including beaver-created ponds (Grasse 1951). These animals tend to concentrate nutrients while feeding, and return them back to the wetland as fecal matter (Kadlec 1979). By clipping standing vegetation and increasing soil nutrient concentrations through defecation, herbivores may actually increase primary production (Batzli 1981).

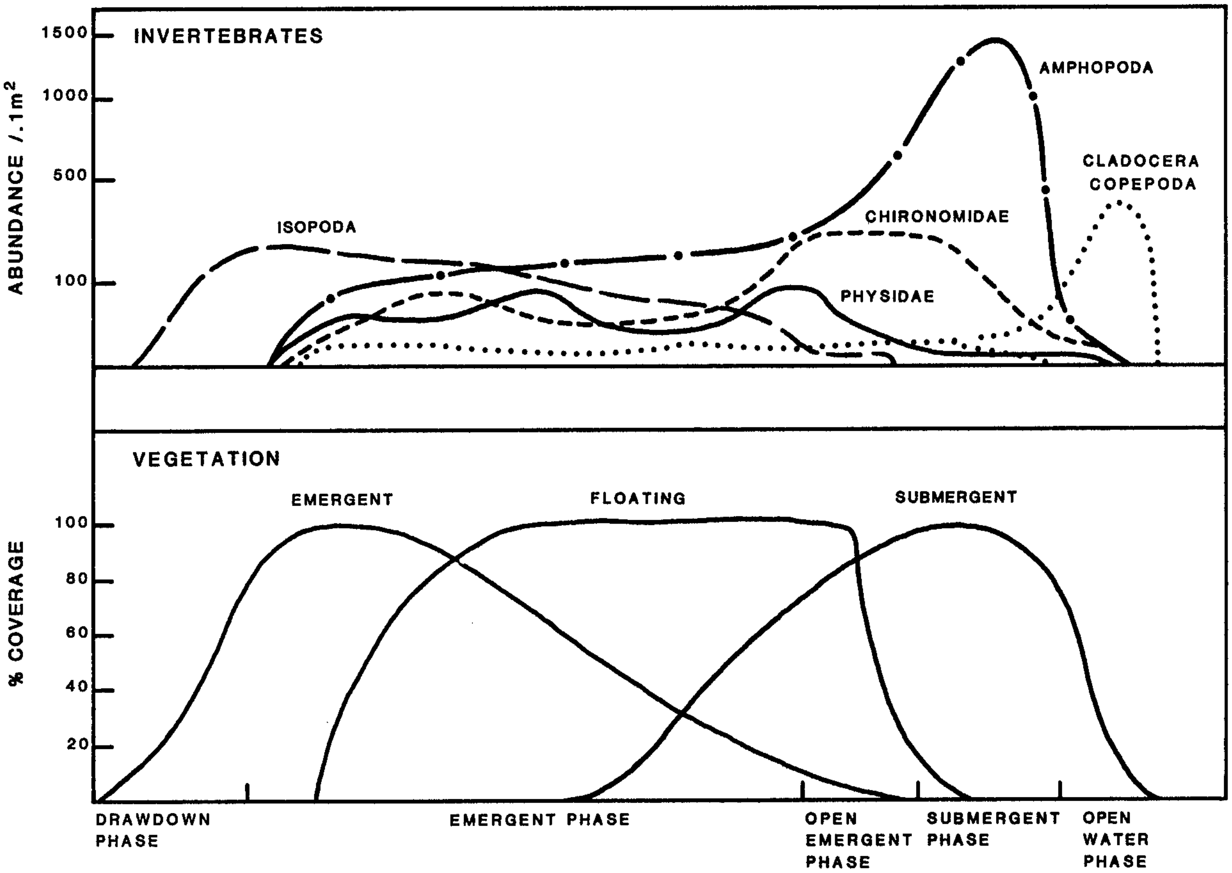


Figure 74. Generalized vegetation-phytomacrofauna associations along a gradient of natural vegetation change in an Iowa marsh. (From Voights 1976.)

Waterfowl and other birds use wetlands for feeding on submerged macrophytes and invertebrates (Krull 1970; Voights 1976), as well as nesting and a place of refuge from predators (Gorenzel et al. 1981). Nutrient enrichment by bird guano can also increase primary production of wetland plant species (Onuf et al. 1977; Kadlec 1979; Odum et al. 1984). Knopf (1985) identified 124 bird species from 6 elevations ranging from 1200 - 1275 m (3,937 - 4,183 ft) along the Platte River drainage of the Colorado Front Range. He found more species diversity below 2000 m (6,562 ft), where willow and cottonwood trees dominated the riparian woody vegetation.

4.5 EFFECTS OF FIRES ON WETLANDS

Fire plays a significant role in the ecology of the Rocky Mountains (Daubenmire 1943). Lightning strikes during summer thunderstorms are the principal agent. In the 5-year period from 1948-1952, lightning strikes caused an average of 3,500 fires per year in 10 Rocky Mountain States. The majority of strikes were on the upper third of the slope (Komarek 1968).

The effect of fire on wetlands is variable. Fire reduces nesting sites for birds while creating open-water areas. Shallow pools are formed where humus and peat have burned. Burning organic matter increases concentrations of soluble ammonia, phosphorus, potassium, calcium, magnesium, sodium, and sulfur. Volatized nitrogen and sulfur, and ash carried away by surface runoff, are the major nutrient losses (Wright and Bailey 1982). A large fire in a Michigan wetland resulted in greater fish biomass in burned areas, presumably due to increased algal production. Alkalinity, pH, and conductivity changed very little because rainfall and runoff after the fire washed out measureable effects on water chemistry. Since the fire was patchy in coverage, habitat diversity increased for larger organisms (Anderson 1982).

CHAPTER 5

WETLAND VALUES[1]

5.1 INTRODUCTION

Publication of the U.S. Fish and Wildlife Service National Wetland Inventory (Shaw and Fredine 1956) brought attention to the threatened status of National wetlands. One of the major findings of the inventory indicated that 40% of the Nation's wetlands had been altered or destroyed by a variety of causes and that additional acreage was being lost at an alarming rate each year. Wetland functions and values began to be recognized, and government and private interest and emphasis changed from one of wetland destruction to protection, reclamation, enhancement, and preservation. Therefore, this chapter attempts to: (1) review the various meanings of the term "value" that have lead to semantic confusion in discussion of wetland values; and (2) present a scientific literature analysis of wetland values within the Rocky Mountain Province.

"Value" and "valuation" are terms commonly used in contemporary culture, with multiple and often confusing meanings. Value (worth of a thing) has specific interpretations in the fields of economics, science, theology, philosophy, psychology, and social sciences, many of which further define levels or realms of value, such as market value, personal value, social value, moral value, and natural value. In Latin, Middle French, and Middle English value meant worth, as in economic or quasi-economic fair exchange for goods or services (Frankena 1967). To this day, economists define value narrowly and strictly by the amount of money a person is willing to surrender to obtain something, in a context of alternative choices and associated prices. Economists observe the ways people prioritize acquisition of goods and the sums of money spent for them, impute value from these observations, and predict or simulate how people would behave in a perfect marketplace, if one were available (Peterson 1985). Plato and other pre-19th Century philosophers distinguished economic value from questions of what was or should be good, right, worthwhile, beautiful, true, or valid. A general theory of value (axiology), grouping these considerations in the same guild, emerged in the mid-19th century. Value theory became popular in philosophical circles in pre- and post-World War II United States and Latin America (Frankena 1967).

Several decades later, Aldo Leopold (1949) and Rachel Carson (1962) jolted society into recognizing the ecological connectedness of all living things and the dire consequences of continued degradation of the natural environment. The seed was sown for the new "environmental ethic." It was argued that man is responsible for protecting the integrity and well-being of

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ecosystems and biological communities because human health and prosperity are made possible by the beneficial consequences of a healthy and stable global ecosystem, of which we are a part.

The "Respect for Nature" and "Dominion Over Nature" doctrines have been discussed at length in the literature (Nash 1972; Dodson-Gray 1981; Routley and Routley 1979; Willard 1980; Willard et al. 1980; Rolston 1981; Taylor 1981; Attfield 1983; Elliott and Gare 1983; Mannison 1983). The controversy is a manifestation of disagreement in Western Society over what is of value, to whom is it of value, and equity (i.e., if two items are assigned equal value, which interested party's preferences hold the most weight in the policy-making arena).

There are those who insist that natural objects and processes have intrinsic or inherent value independent of human cognition and preference. That is to say, they have value based upon their essential nature or constitution. Alternatively, it is also argued that nothing is of value until it is perceived to be so by a member of the human species, which is unique in its capacity to make this distinction. Man has, by Judeo-Christian tradition, assumed an inalienable right to manipulate and subvert the natural world for his greatest gain. Wetland goods and services that are useful to man are considered to be of socio-economic value. This category of value lends itself to scientific study and is the main emphasis of the following discussion.

5.2 INTRINSIC WETLAND VALUES

Intrinsic worth of a natural object or process is essentially a philosophical concept. No amount of dissection or experimentation will ever confirm or deny its existence. Since it lies outside the realm of human sovereignty, it is extremely difficult to incorporate into a multiple objective scenario for socio-economic problem resolution. However, a belief in inherent worth of ecosystem components shapes the values of some who argue for wetland preservation. A few commonly argued justifications for this view follow.

In the biocentric view the well-being of every wetland organism, and the stability of all ecological function should be promoted in recognition of each one's intrinsic good. Since humans are thought to be ruled by the same laws of genetics, natural selection, and adaptation as all other organisms, there are no grounds for human chauvinism or dominion over nature. In fact, while *Homo sapiens* is dependent upon Earth's community for survival, the biosphere has and, no doubt, will continue to function well in man's complete absence (Willard et al. 1980).

The human species is a relative newcomer to the evolutionary arena. Long before the evolution of human cognition, cells had biochemical and genetic "linguistics" for communicating within and amongst themselves. Evolutionary mechanisms "solved problems" through natural selection and adaptations, and cottonwood and protozoans held genetic "memories" of their ancestors. Plant growth form followed Fibonacci's numbers, cells recognized certain molecular shapes, and RNA "translated" the DNA code into amino acid sequences hundreds of millions of years before humans "discovered" these patterns intellectually. Humans may be temporary, albeit very influential, beneficiaries of wetland

goods and processes (Rolston 1981). In this view, nature is the values carrier. Rather than our bestowing value on nature, nature gives value to human life (Rolston 1982).

The biocentric attitude may be a salient consideration when wetland destruction is mitigated by construction of a "new" wetland in another location, or when mining in a wetland is followed by restoration work. It has been argued that the intrinsic value of the natural wetland is in its unique genesis, in its continuity with its past. Even if a new or restored wetland were structurally and functionally identical to the one destroyed, the trade would not be a fair one, because the history cannot be reconstructed. A reconstructed wetland may have diminished value, just as a forged painting does. Therefore, for those who express a human preference of recognizing intrinsic value in wetlands, there is a vast difference between preventing damage to wetlands and repairing damage once it is done or creating a wetland elsewhere (Elliott 1982).

5.3 SOCIO-ECONOMIC BENEFIT VALUES

Socio-economic values are assigned to all beneficial consequences to society from existing wetland functions and components. The following general categories of socio-economic values have been identified for discussion in this section: (1) ecological values, (2) experiential values, (3) scientific values, and (4) economic values (Figure 75).

Socio-economic values attributed to wetlands vary with human educational background, experience, and knowledge about the environment, together with scarcity of wetland resources and their biota. Defining and identifying these values and functions is addressed well by several authors (Darnell 1979; Odum 1979; Friedman and DeWitt 1979; Foster 1979; Adamus and Stockwell 1983; Kusler 1983; Office of Technology Assessment 1984; Tiner 1984).

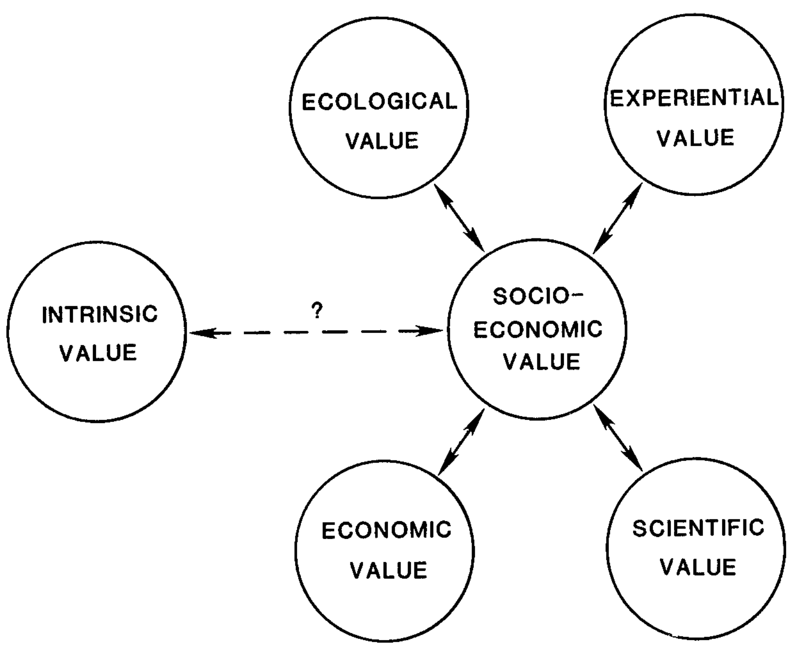

Figure 75. Categories of wetland values.

Ecological Values

Wetland ecological processes provide a variety of global, regional, and local maintenance-free services from which society benefits at no cost. Disruption of wetland ecological integrity curtails many of these services. In this event, society must go to great expense to develop technological means for reinstating the services if, in fact, a technological solution is feasible. In light of the high cost and dubious success of artificially replacing wetland ecological value, efforts are being made to identify the monetary value of *in situ* natural wetland goods and services.

Very little research has been done on the structure and functions of Rocky Mountain wetlands. It is assumed in this discusson that functions and values identified in research in wetlands in other regions of North America may be applied conservatively to Rocky Mountain wetlands with a reasonable level of reliability. Specific examples germaine to montane and subalpine wetlands are included whenever possible. Beneficial products of these wetlands are as follows:

(1) atmospheric, climatological, and meteorological stabilization,

(2) ground water discharge and recharge,

(3) flood control,

(4) erosion control,

(5) water purification,

(6) nutrient accumulation and cycling,

(7) primary production,

(8) secondary production, and

(9) wildlife refuge.

Atmospheric, climatological, and meteorological stabilization. Earth's wetland surfaces have an effect on local and regional climatological and meteorological phenomena of moderating air temperatures, contributing water vapor to the atmosphere, and producing gases from nutrient decomposition and cycling processes. Rocky Mountain wetlands contain cold water year round and they warm and cool less rapidly than surrounding uplands. For this reason, and because wetlands lie in valley floors where cool air drains, uplands adjacent to wetlands remain cooler during summer months. Large lakes are heat sinks, which warm gradually in spring, store heat all summer, and cool gradually in the fall. If the volume of water contained in lakes is great enough, lakeside temperatures may remain cooler in the spring and warmer in the fall than regional temperatures.

During snow-free seasons, wetlands may augment local precipitation by contributing water vapor to the atmosphere from open water, saturated soils, and evapotranspiration from plants (Ives 1942a; Gannon et al. 1979; Office of Technology Assessment 1984). On summer afternoons in the Rockies, water vapor lifted from the terrain cools, forming cumulus clouds over mountain peaks. Closed circuit convection systems produce thunderstorms, hailstorms, and electrical activity (Ives 1942a; Marr 1967). In Florida, lakes larger than a mile in diameter have more cumulus cloud formation than smaller lakes (Cowardin et al. 1979). It was hypothesized that drainage of Florida wetlands would result in reduced regional precipitation. Rocky Mountain watersheds where wetlands have been drained and transbasin water diversions made, both of which reduce total stream discharge and lower the wetland water table, may also have less cumulative precipitation.

No work has been done on the contribution of Rocky Mountain wetlands to the maintenance of global atmospheric stability. Wetland research elsewhere suggests such a function. Microbial decomposition of wetland organic matter in the absence of oxygen produces many gaseous by-products, such as methane, hydrogen sulfide, and carbon dioxide (Odum 1979). Methane gas may act as a homeostatic regulator on the ozone layer in Earth's upper atmosphere, which protects life from the harmful effects of ultraviolet radiation (Odum 1979). Disruption of wetland soils exposes reduced carbon in peats and highly organic soils to oxygen. Resulting oxidation reactions release carbon dioxide to the atmosphere. This, combined with destruction of wetland vegetation that consumes carbon dioxide during photosynthesis, may cause global warming (Odum 1979). Nitrous oxides produced by human activities may adversely effect ozone stability and thus, Earth's radiation budget. Microbes have been found to decompose or transform nitrous oxides in anaerobic wetland soils of tidal salt marshes (Office of Technology Assessment 1984).

Groundwater recharge or discharge. Some wetlands are of value in recharging or discharging aquifers (Odum 1979; Kusler 1983; U.S. Office of Technology Assessment 1984). Water may move into the water table both by infiltration from the surface through an unsaturated zone and by seepage from streams, lakes or confining basins. Recharge may take place through bottom substrates of western mountain streams (Leopold and Miller 1961). Wetlands with deep peat deposits are unlikely recharge areas, since the undecomposed organic matter in peat has a low permeability and high water retension (Carter et al. 1979). In peats of a Wyoming mountain bog, hydraulic conductance was very low, ranging from 0.0239 cm (0.0094 in) per day at a 46 cm (18 in) peat depth to 0.0161 cm (0.0063 in) per day at a 91 cm (36 in) depth (Sturges 1968). Uplands were found to play a larger role in recharge than peatlands in three Minnesota watersheds (Carter et al. 1979).

It is likely that long wetland-covered valley floors between mountain ridges throughout the Rockies contain large quantities of water. The interchange of water between surface and interstitial compartments and deeper aquifers has not been documented. The extent of aquifer draw shown for agricultural irrigation in the San Luis Valley of Southern Colorado, an intermountain basin, has threatened the Alamosa/Monte Vista Wildlife Refuge, where water must be pumped from the aquifer to maintain the wetlands. This suggests that discharge of water from the aquifer has been important for the natural maintenance of these particular wetlands. This refuge is a migratory resting area for the endangered whooping crane.

Flood control. Wetlands are of value in providing natural channels for flood waters and in attenuating flood peaks by temporarily slowing and storing water (Figure 76) (Carter et al. 1979; Jarrett and Costa 1984). Effectiveness of flood control is dictated by total wetland area, type and condition of vegetation, valley slope, location of wetland in the flood path, magnitude of flood, degree of encroachment on the wetland, and saturation of wetland soils before flooding (Carter et al. 1979; Office of Technology Assessment 1984).

Hydrological and geological studies of the Lawn Lake and Cascade Lake Dam failures in Larimer County, Colorado, illustrate the importance of wetlands in moderating Rocky Mountain flood damages (Figure 77). Just before dawn on July 15, 1982, an earthen dam on Lawn Lake at 3,351 m (10,987 ft) in Rocky Mountain National Park suffered a valve failure and consequent dam erosion and collapse. Suddenly, 674 ac-ft of water were released into the Roaring River, forming a wall of water 7.5 to 9.2 m (25 to 30 ft) high containing a discharge of 504 m^3 (18,000 ft^3) per second and moving at 14.6 km (9.1 mi) per hour downstream. After dropping 732 m (2,400 ft) in 7.6 km (4.75 mi), the flood wave entered Fall River at Horseshoe Park. Here, the flood wave spread out on the broad, flat valley and was attenuated by vegetation (Figure 78) before finally reaching Cascade Lake Dam immediately downstream. The height of the wall of water was reduced to about 3.1 m (10 ft) and the water spread out over the meadow to a width of 397 m (1,300 ft). Breaching of Cascade Lake Dam from added pressure let loose a second wave of floodwater that made its destructive path down Fall River and through the City of Estes Park. The flood was finally contained by Olympus Dam on Lake Estes. It had lasted 3 hours and 40 minutes, claimed 4 lives, and caused 31 million dollars in damage in public and private property and in clean-up and subsequent economic losses. This was the largest flood to occur on Roaring River and Fall River since the retreat of the glaciers 10,000 years earlier (Jarrett and Costa 1984).

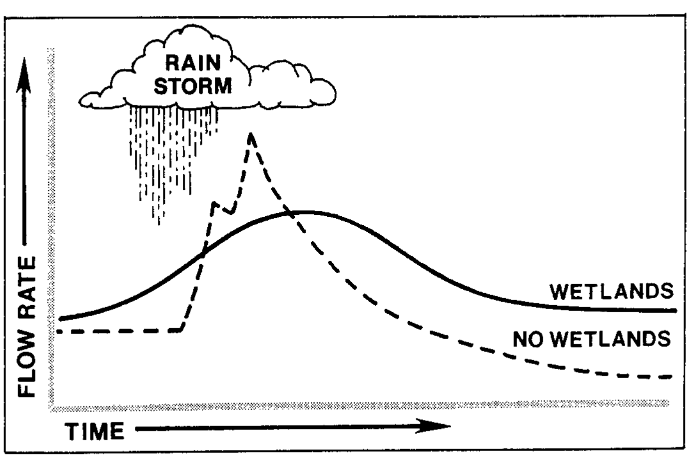

Figure 76. Wetlands reduce peak flows. (From Kusler 1983.)

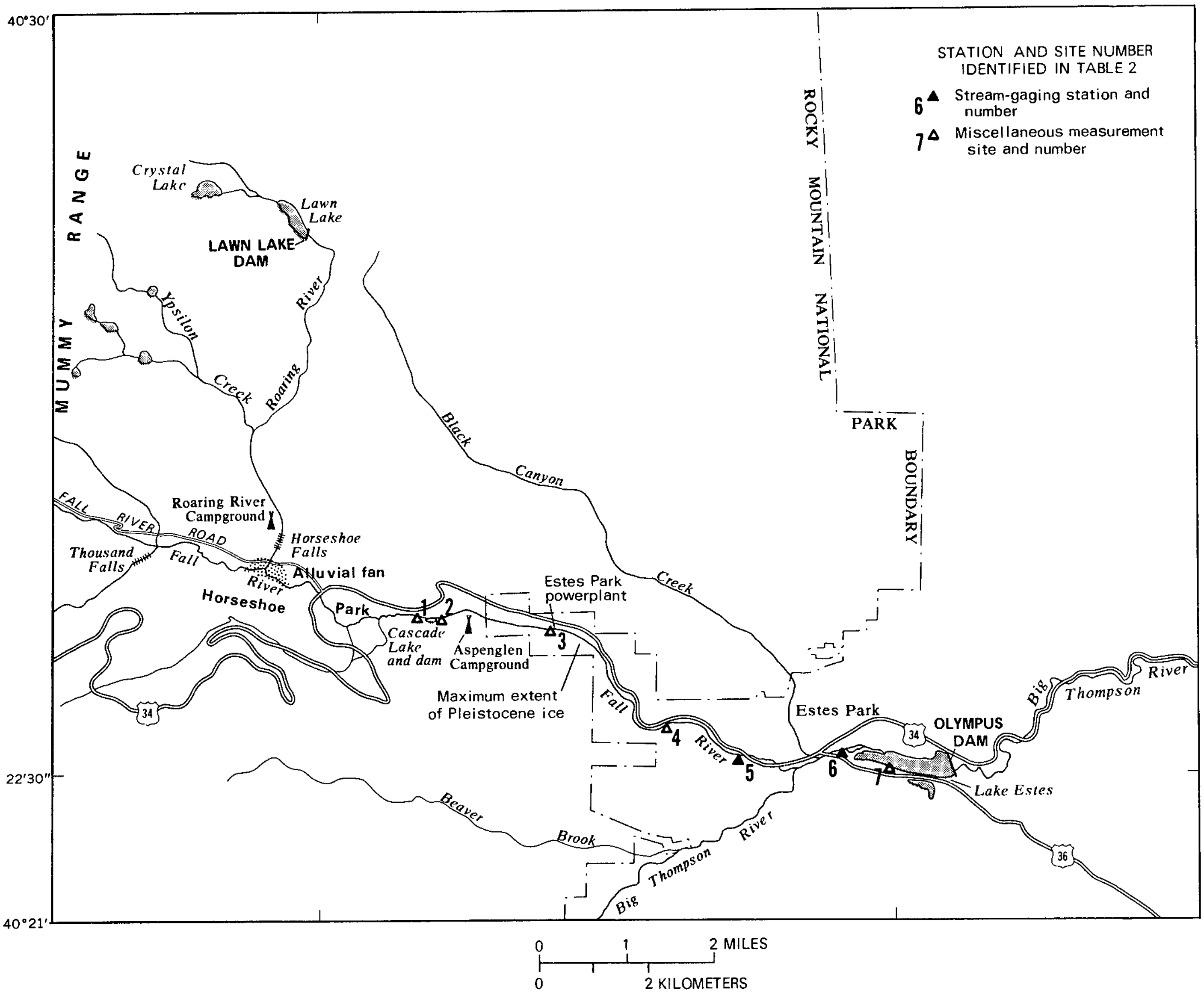

Figure 77. Map of area affected by the Lawn Lake Dam and Cascade Lake Dam failures in Rocky Mountain National Park, Colorado, on July 15, 1982. (From Jarrett and Costa 1984.)

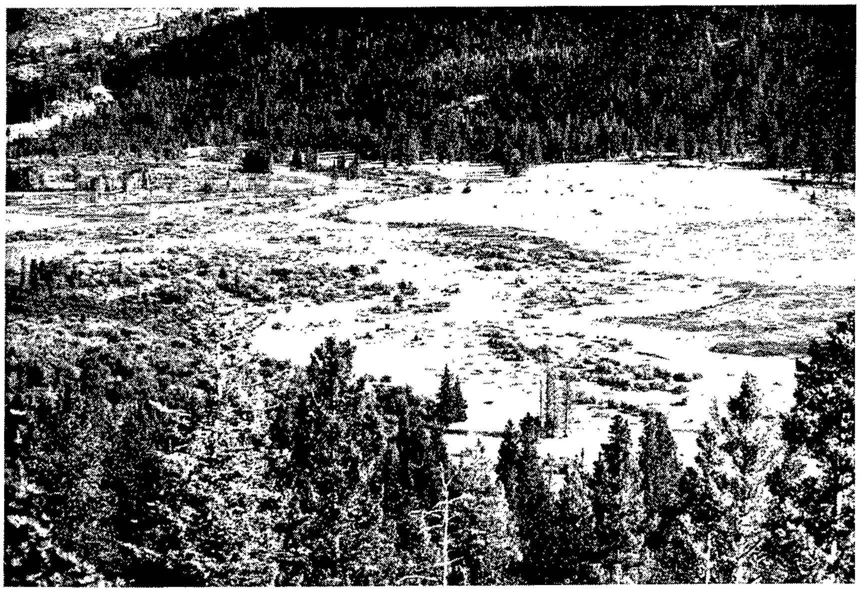

Figure 78. Flood waters were attenuated by wetland vegetation and reduced to a quiet lake while passing through Horseshoe Park following the 1982 Lawn Lake Dam failure in Rocky Mountain National Park. (Photo by D. F. Atkins.)

If it were not for Horseshoe Park on Roaring River above the City of Estes Park, flood peak, flood damage, and loss of life would have been much worse (Jarrett and Costa 1984). Horseshoe Park contains cohesive silts and clays that were deposited on the floor of a Pleistocene moraine lake, which eventually filled with alluvium and drained. The flat moraine-rimmed basin is 0.8 km (0.5 mi) wide and 4.8 km (3 mi) long, with an average slope of 0.7% (Figure 79). Meadow grasses, reeds, and dense willow stands cover the wetlands adjacent to the tortuously meandering Fall River that bisects the park. Few Colorado Front Range valleys have such extensive meadows and wetlands (Jarrett and Costa 1984).

The Lawn Lake flood waters passed over the park, crossing stream meanders and reaching a depth of 3.1 m (10 ft) and a width of 397 m (1,300 ft). The following conclusions were drawn about the value of this basin in controlling the flood (Jarrett and Costa 1984):

1. A wall of water 7.5 to 9.2 m (25 to 30 ft) high was reduced to a tranquil and smooth lake as the flood peak passed through the park (Figure 80).

2. Flood velocity in the upstream Roaring River was 14.6 km (9.1 mi) per hour. It was reduced to 3.4 km (2.1 mi) per hour in the park.

3. Horseshoe Park attenuated the flood because of its low gradient, flood plain width, and very dense wetland shrub growth.

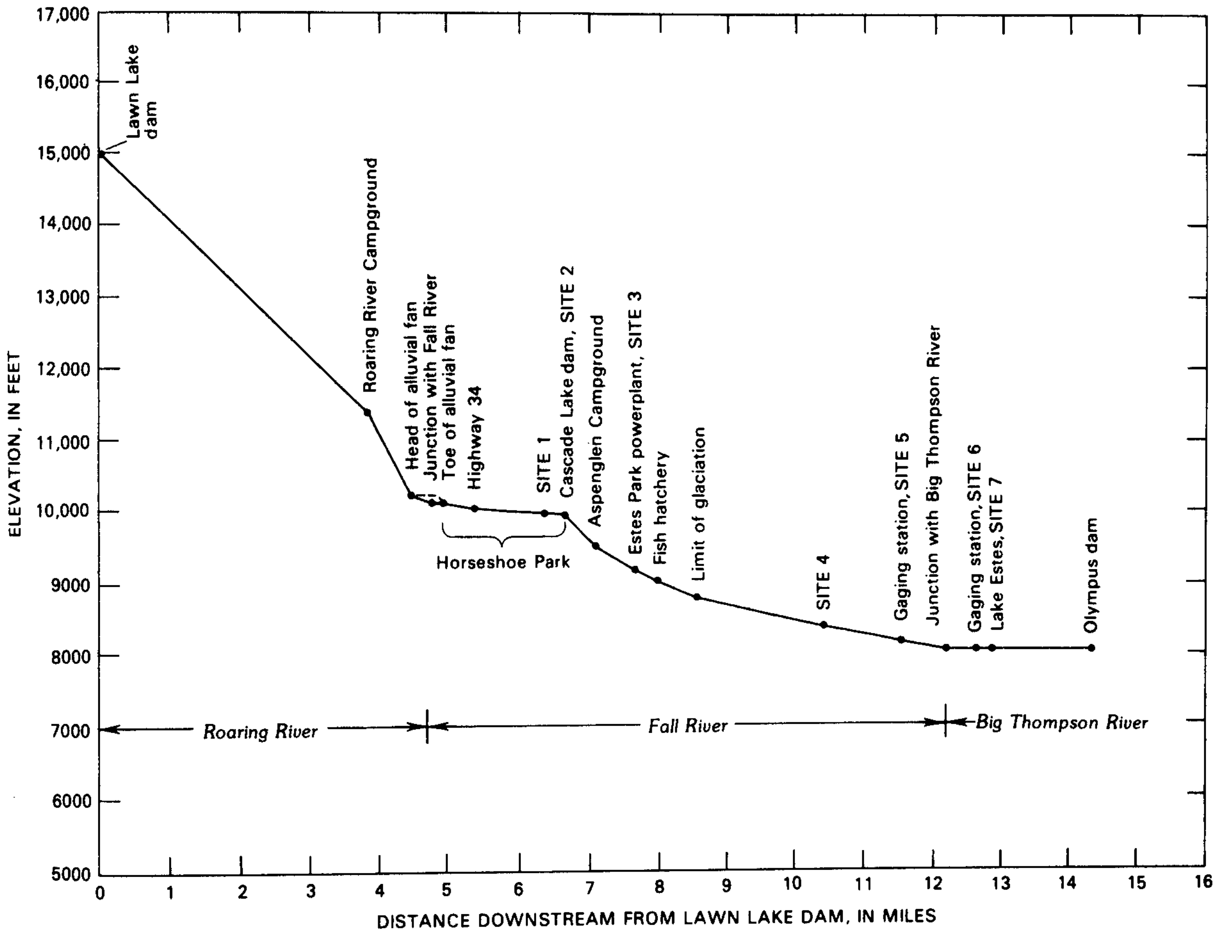

Figure 79. Long profile of flood path of the water from Lawn Lake Dam and Cascade Lake Dam failures. Vertical exaggeration 10.5 times. Horseshoe Park contrasts with upstream and downstream reaches in its flatness. (From Jarrett and Costa 1984.)

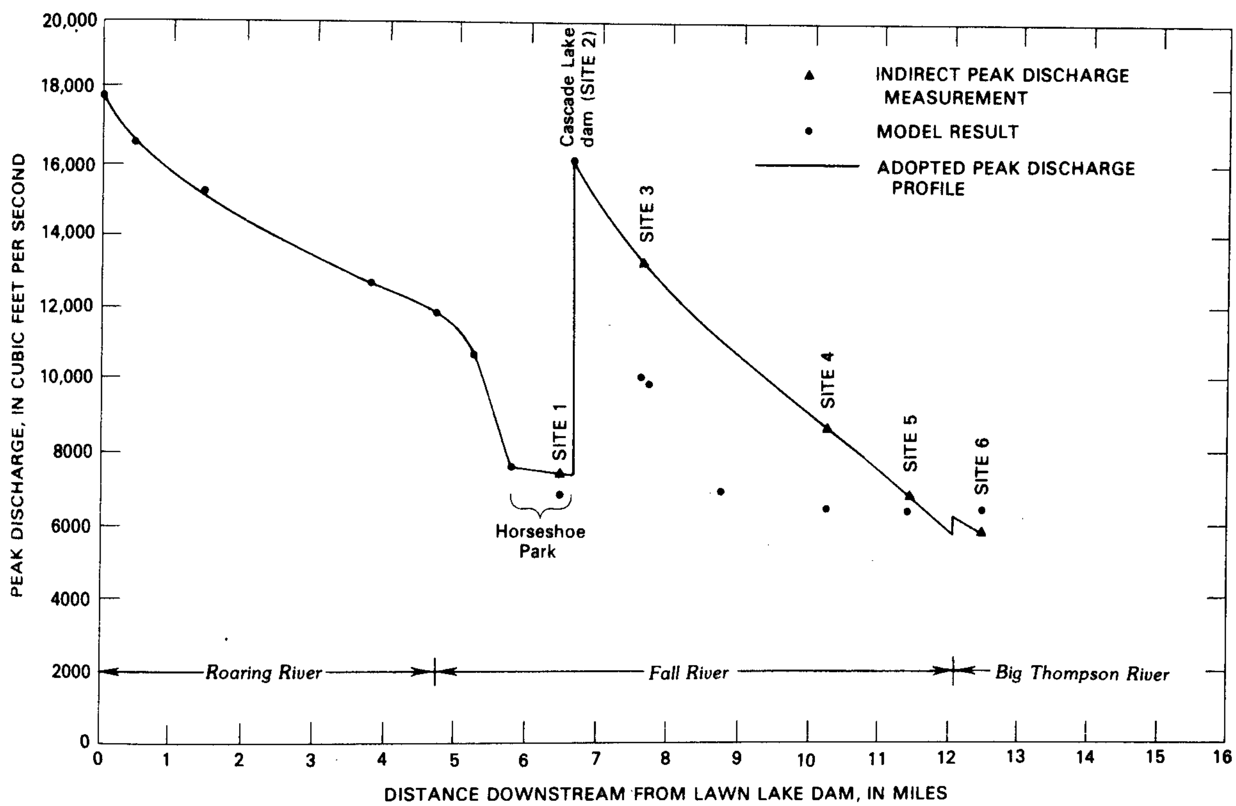

Figure 80. Peak-discharge profile based on indirect peak-discharge measurements and model results. Indirect measurements are believed to be more accurate than dam-break model results. Horseshoe Park reduced a wall of water to a quiet lake. (From Jarrett and Costa 1984.)

4. While Horseshoe Park absorbed and slowed the flood waters, downstream residents and businesses were given precious time to prepare for the onrush of water (Figure 81).

In a Wisconsin study (Novitzki 1979), peak stream discharge was significantly lower in basins with large lake and wetland areas than in basins with little or no wetland area. Consequently, loss of wetland from basins with already limited wetland surface area was expected to have a greater impact on stream discharge than in those with a large wetland area. It is likely that this hypothesis would hold in the Rocky Mountain region.

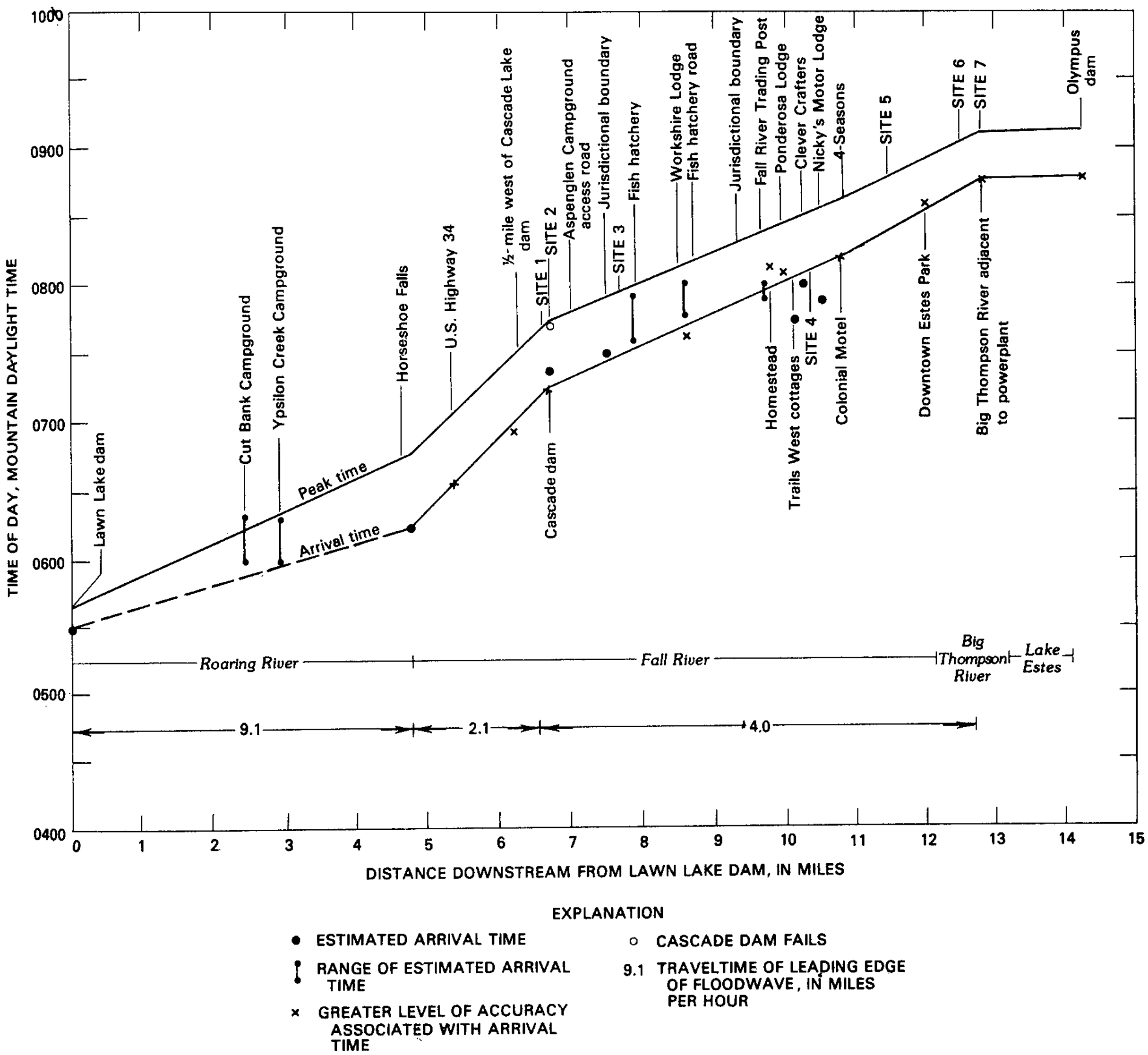

Figure 81. Arrival time, peak time, and travel speed of leading edge of flood wave of July 15, 1982. (Modified from Graham and Brown 1983.) Horseshoe Park slowed flood travel speed providing Estes Park residents time to prepare for the approaching flood.

Erosion control. Wetland vegetation on river banks and lake shores helps to prevent shoreline erosion and protect neighboring uplands. Low gradient shorelines and vegetation cover dissipate and absorb wave and current energy (Figure 82). Rooted vegetation is especially important in binding and stabilizing soils. Denver suburban development has removed vegetation from large areas and created serious erosion problems. At one study site, sediment production increased 30 times, and was accompanied by increased stream discharge, soil erosion, wind blown dust, and floodplain spreading. Old flood plain surface area was increased by 270% as a result of up-stream vegetation removal and soil disturbance (Graf 1975).

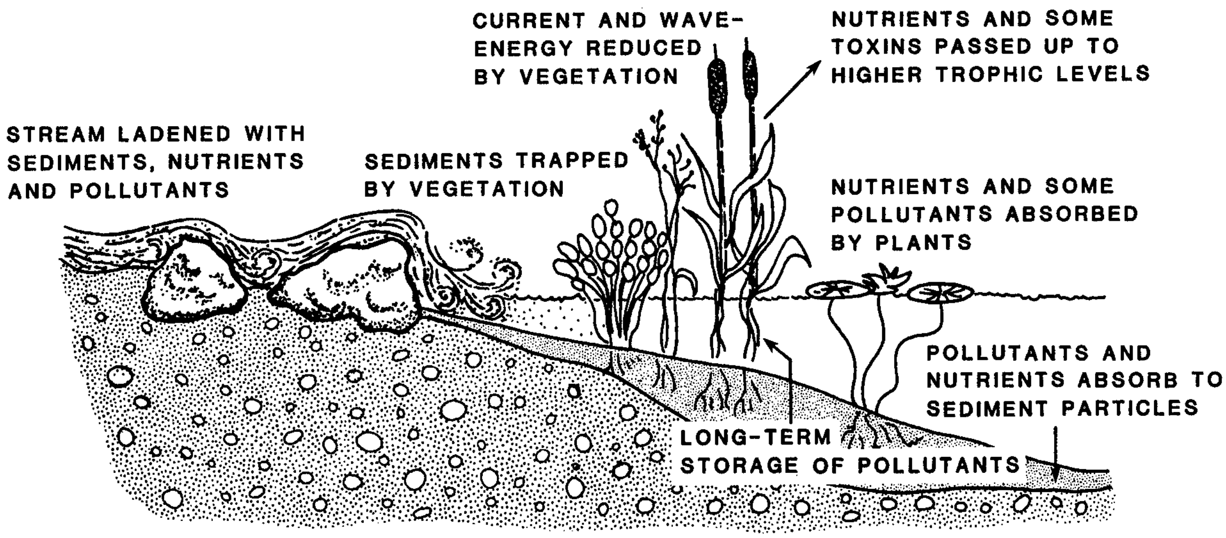

Figure 82. Wetland vegetation prevents erosion, traps sediment, and improves water quality. (Adapted from Kusler 1983.)

The stability and resiliency of natural wetland vegetation is remarkable. In the 1982 Roaring River flood and the 1976 Big Thompson flood, trees held firm where structures did not. In the 1982 flood event caused by the dam failures in Rocky Mountain National Park, erosive forces were not sufficient to reform vegetated stream channel meanders in low-gradient Horseshoe Park. One week after the flood, aerial photographs showed no visible modification of surficial geology (Figure 83) (Jarrett and Costa 1984).

There is a limit to the soil-holding capacity of wetland vegetation. In higher gradient stream reaches up- and down-stream of Horseshoe Park, flood discharge and velocity were so great that vegetation was entirely removed from stream banks and the stream bed morainal material was scoured to depths of up to 10.7 m (35 ft) (Figure 84) (Jarrett and Costa 1984).

Water purification values. A combination of low gradient and emergent vegetation in wetlands reduces both water depth and velocity, creating good depositional environments (Figure 82). Water burdened with suspended sediments, toxins, pollutants, and pathogens is cleansed as it flows through wetlands. If a wetland has no outlet, sediments gradually fill the basin. In the Rocky Mountain region, pollutants enter wetlands from municipal and industrial wastes, paved surfaces, sewage sludges, mined land drainage, eroding stream banks, and the atmosphere.

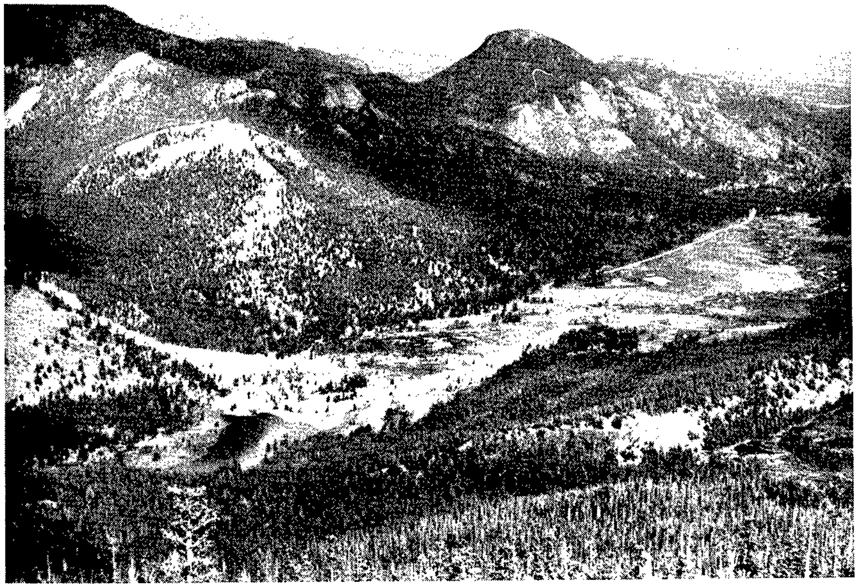

Figure 83. Aerial view of Horseshoe Park, Rocky Mountain National Park, following 1982 Lawn Lake flood. Large organic debris and sediments were captured in upstream end of Horseshoe Park near confluence of Roaring River and Fall River where alluvial fan formed a new lake. Surficial geology and vegetated stream meanders were not modified by flood in downstream regions of Horseshoe Park. (Photo by B. Willard.)

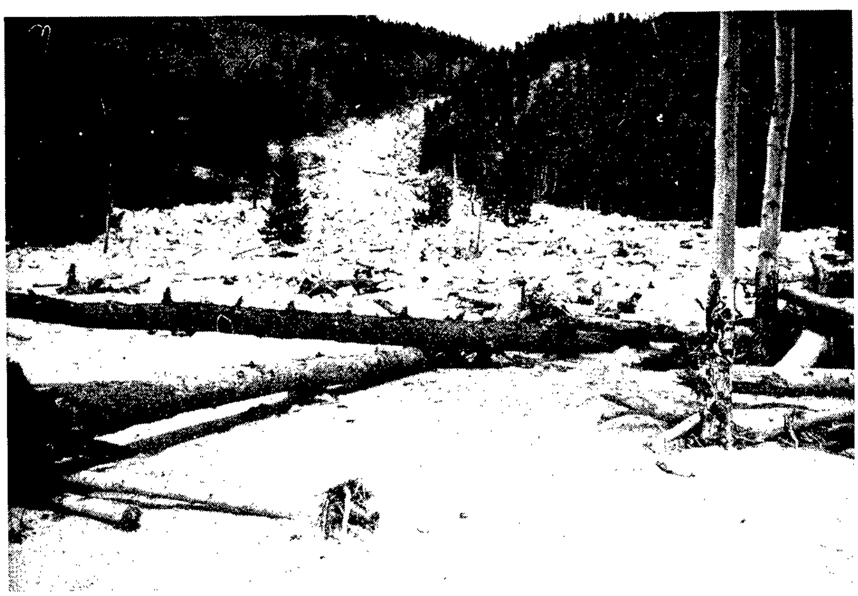

Figure 84. Alluvial fan left by Roaring River during Lawn Lake flood. Flood discharge and velocity were so great in high gradient stream reaches upstream of Horseshoe Park that vegetation was stripped from stream banks and streambed morainal deposits scoured to depths of up to 10.7 m (35 ft). (Photo by B. Willard.)

High levels of suspended material (turbidity) in the water column impair aesthetic visual quality, dissolved oxygen concentrations, fish spawning, and benthic invertebrate and plant productivity. Vegetated wetlands are more successful in reducing turbidity than nonvegetated areas. During the 1982 Lawn Lake flood in Rocky Mountain National Park, most large organic debris was captured in the upstream end of the Horseshoe Park wetland and very little sediment was carried below it (Figure 83) (Jarrett and Costa 1984). Discharge from Wisconsin watersheds containing wetlands was 90% lower in suspended sediments than from those with no wetlands (Novitzki 1979).

Wetland sediments serve as a primary and secondary sink for pollutants. Pathogens, heavy metals, chlorinated petroleum, and hydrocarbons adsorb to organic and inorganic sediments (Carter et al. 1979; Kusler 1983; Office of Technology Assessment 1984). Upon deposition, they move into detritus-based food webs, are assimilated by plants, exported by scouring flood waters, or remain permanently in sediments. If biodegradable toxins, such as malathion, heptachlor, lindane, or enderin are given an adequate residence time in the sediments, they may be rendered harmless (Office of Technology Assessment 1984). Refactory chemicals, such as DDT, hydrocarbons, or halogenated hydrocarbons with lasting toxic properties, may persist in sediments or be incorporated into organic molecules in the food web.

Heavy metal accumulation was demonstrated in several Colorado Front Range wetlands (Sarnecki 1983). Wetland efficiency in heavy metal removal ranges from 20% to 100% and varies with metal type involved and hydrological and biological characteristics of the wetland (Tchobanoglous and Culp 1980; Office of Technology Assessment 1984). The fate of heavy metals in sediments and food webs is not clearly understood but there is evidence that they concentrate up the food chain (Kibby 1978; Kadlec and Kadlec 1979).

Standing vegetation, litter, and moss in a Wyoming mountain bog were efficient, from a public health standpoint, in removing radionuclides from snowmelt water (Sturges and Sundin 1968). Sedge mats on wetlands on Niwot Ridge, Colorado, were demonstrated to remove 100% of radionuclides from snowmelt water (Osburn 1963, 1969).

Wetlands in some parts of the country are used as secondary and tertiary wastewater treatment sites (Gosselink et al. 1973; Ryther et al. 1979). Wetlands in contact with aquifers are at risk of releasing infectious agents into aquifers, and ultimately into potable water supplies. It is important to know the survivorship of pathogenic bacteria and viruses in the wetland environment before this practice becomes more widespread (Kadlec and Kadlec 1979).

To summarize, it is not known what load of contaminants wetlands may receive without impairment of their natural functions, nor is it known to what degree or for how long they are capable of storing or degrading toxic pollutants (Kadlec and Kadlec 1979). The role of Rocky Mountain wetlands in carrying out these services is poorly documented. It is safe to say that if contamination of wetland sediments is suspected, they should not be disrupted by dredging or any other means. Such activities run the risk of releasing sediments and adsorbed materials to surface waters and removing their adsorptive capacity from future use.

Nutrient cycling values. Little information is available on the cycling of organic and inorganic substances in Rocky Mountain wetlands. Earlier, literature was reviewed on nutrient cycling in North American wetlands, including specific references to research directly relevant to wetlands in this region. Discussion on the value of nutrient cycling in montane and subalpine wetlands is based on the assumption that cycling processes found in other temperate wetlands can be extrapolated to the Rockies. The socio-economic value of nutrient cycling is largely indirect. It stems from the importance of nutrient accumulation, decomposition, nitrogen fixation, and nutrient exportation to the food chain.

Organic and inorganic matter accumulation occurs in wetlands when plants produced during the growing season die and fall into the sediments. There, nutrients are stored as particulate matter and soluble nutrients are leached from the plant matter. Residence time of this material depends upon wetland basin morphology, hydrological regimes, and decomposition rate. Commonly, accumulation rate surpasses decomposition rate, with a result of gradual build-up of peat and organically bound nutrients in wetland sediments. Peat accumulation is slow, but can be considerable over several thousand years (Friedman and Dewitt 1979). Peats containing pollen and adsorbed elements and compounds are of scientific value as records of wetland age, regional paleobotany, and prehistoric atmospheric climatological change.

Organic matter content of wetland soils is generally higher than that of surrounding ecosystems in the Rockies (Ellison 1954; Boyd 1970b; Chapin 1981). Organic soils are good substrates for plant growth, hold moisture well, and are an important source of nutrients and detritus for organisms within the wetland and in the adjoining ecosystems.

Decomposition of organic matter is accomplished through leaching of soluble substances, fragmentation due to abrasive forces of animal activities and weathering, and by bacterial and fungal action. Decomposition is of value because it releases soluble forms of phosphorus, nitrogen, potassium, carbonates, and other nutrients, which are readily taken up by wetland plants and microorganisms. Decomposition on aerobic surfaces of wetland sediments yields soluble nutrients, organic acids, and gases (e.g., CH_4, H_2S, CO_2) that circulate through the wetland, surrounding ecosystems, and atmosphere. Highest rate of denitrification, which releases free nitrogen to the atmosphere, occurs in carbon-rich, water-logged soils (Tilton and Schweigler 1979).

Detritus is the foundation of the aquatic food web. Dead plants colonized by microbes are the primary food source for immature stages of many aquatic insects and many other invertebrates that will not ingest living plant matter (Fisher and Likens 1973; Cummins 1973, 1974, 1975, 1977; Ward 1985).

Alnus spp., Dryas spp., Juncus spp., and legumes are associated symbiotically with bacteria, in their root nodules, which promote nitrogen fixation (Adamus 1983). This process transforms atmospheric nitrogen, which is of no use to plant or animal species, to nitrates, which are absorbed and assimilated in growth of plants and microbes. Nitrate production is also augmented by bacteria that oxidize ammonia produced in animal feces and by microbial activity.

Wetlands are valuable as exporters of decaying plant matter to other ecosystems. Immature aquatic insects remove energy and nutrients from the wetland as they emerge as winged adults and become part of the terrestrial food chain. Birds and mammals feeding in wetlands export nutrients when they defecate or die in surrounding ecosystems. Hydrological events commonly flush organic sediments from wetlands into adjacent streams and ultimately the ocean. Wetlands associated with riverine ecosystems in the Rockies must play a vital role in augmenting fine and particulate organic matter consumed by protozoans and benthic invertebrates finely adapted to utilize narrow ranges of food particle sizes (Fisher and Likens 1973; Cummins 1973, 1974, 1975, 1977). This is critical to the survival of avian, mammal, amphibian, reptile, and fish populations.

Primary production values. Photosynthetic reactions in wetland plants make wetlands the most productive ecosystems on land (Figure 85) (Odum 1979). Comparisons of productivity rates of Rocky Montain wetlands to those of other regions of North America are impossible due to the paucity of reported research. Wetland plants have abundant water, a rich nutrient supply, and diverse adaptations for surviving floating, submerged, or seasonally flooded in water (Richardson 1979). For these reasons, Rocky Mountain wetlands are probably more productive of plant biomass than are surrounding terrestrial ecosystems in this semiarid climate.

Figure 85. Rooted floating-leaved plant Nuphar polycepalum in subalpine moraine pond. Wetlands sustain high primary productivity. (Photo by S. Foster.)

The value of primary productivity is in the direct and indirect relationships of plant morphology and biomass to higher levels in the food web. Wetland plants are valuable as (1) food source, (2) substrate for plant and animal growth, (3) detritus source, (4) animal shelter and nesting material, and (5) sediment traps.

Live wetland plants are a primary food source to beaver, muskrat, adult surface-feeding ducks (Figure 86), swans, geese, and some invertebrates, to name a few. Bacteria, other microorganisms, and larger animals utilize "periphyton," the assemblage of diatoms, blue-green, and green algae attached to submerged logs, leaves, and stems (Ward 1985). Decaying plant material (detritus) is essential to many aquatic invertebrates, which ingest both the plant fiber and associated microbes.

Many animals find protective cover from predators in wetland vegetation. For instance, common snipe (Capella gallinago), nesting female ducks, green damselflies, and leopard frogs are behaviorally and morphologically camouflaged in wetland vegetation and associated shadows. Immature insects seek refuge from currents in rooted and submerged vegetation. Some water mites and a water beetle lay eggs in plant tissues (Klotts 1966). Plant materials are used by caddisfly larvae to construct portable cases, and several moths, beetles, midges, and mosquitos obtain oxygen directly from submerged plant tissues. Waterfowl nests and lodges of beaver and muskrat are constructed from wetland vegetation.

Plants in wetlands play an important part in nutrient cycling. Rooted vegetation also slows water velocity in floods, prevents soil erosion, and traps sediments from turbid water.

Figure 86. Mallard ducks (Anas platyrhynchos) surface feeding on submerged plants and invertebrates. (Photo by Ben Foster.)

Secondary production values. Secondary productivity refers to the capacity of an ecosystem to partially or completely sustain animal life cycles and populations. It is estimated that as many as 900 animal species in the United States require wetlands for survival. Wetlands in the semiarid Rocky Mountains are virtual oases for wildlife because of their high productivity, habitat diversity, and abundant water supply in the midst of a less productive, drier landscape. While some animal species are bound to wetlands throughout their life cycles, transient wetland visitors have an opportunity to enlarge their populations and expand their geographic distribution (Crow and MacDonald 1979).

The value of wetlands to animals depends on the interaction of many variables (Kusler 1983). Some of the most important features include:

(1) amount of open water and arrangement of vegetation around it;

(2) diversity of wetland vegetation and distribution of plant associations;

(3) size of wetland and accessibility to surrounding habitats;

(4) proximity to other wetlands, lakes, streams, and other topographic features;

(5) water chemistry and water permanence; and

(6) frequency and severity of water level fluctuations.

Modes of energy transfer and resource utilization patterns, including temporal uses, are summarized for North American wetlands in Table 36. Energy flows through wetland ecosystems by direct consumption of primary consumers, predation, detritus export, leaching of dissolved organic compounds from plants and from animal excretions, and by export of larvae and juveniles. Resources utilized include foods (nutrients and energy) and nontrophic opportunities of diverse habitat types. Resource utilization by animals may be year round by local residents or seasonal by neighboring populations and migrants. The remainder of this discussion will focus on the importance of these wetland resources to animal life.

a. Modes of energy transfer. Wetland plants are consumed directly by insects, gastropods, fish, reptiles, amphibians, waterfowl, shorebirds, and mammals. In this process, nutrients and energy are transferred from plant tissues to the animal, where some of it is assimilated into consumer's tissues. Many small mammals, including rabbits, hares, voles, and mice venture from their drier upland habitat into the wetland to feed on vegetation (Crow and MacDonald 1979).

Large mammals are also direct consumers of wetland plants. Floodplain communities are particularly important as spring habitat for grizzly bears (Riggs and Armour 1978; Singer 1978). In Glacier National Park, 81% of grizzly bear (*Ursus arctos horribilis*) observations were in wet meadows. With one exception, all observed bears were within 50 m (164 ft) of water. Bears tend

to browse for food in the riparian zone and eat spring shoots of cow parsnip (Heracleum sphondylium) and Angelica spp. in aspen groves and meadows. In midsummer, their tastes turn to fruits, roots, insects, and sedges. Black bears (Ursus americanus) (Figure 87) have similar food preferences, but are restricted to semiopen habitats at mid-elevations. They are rarely seen above 1,800 m (5,906 ft) and seem to be dominated by grizzlies (Schaffer 1971). In the lower 48 States, grizzly bears number fewer than 1,000 and are listed as threatened under the Endangered Species Act of 1973 (Chadwick 1985).

Mule deer and elk frequently browse and graze in wetlands in Rocky Mountain National Park. Winter use of willow and aspen by elk and mule deer is especially heavy where grasses and herbs are less abundant or covered with snow. Snow depth is a primary determinant of habitat selection by mule deer, but they, too, feed frequently in moist bottomlands (Wright et al. 1983).

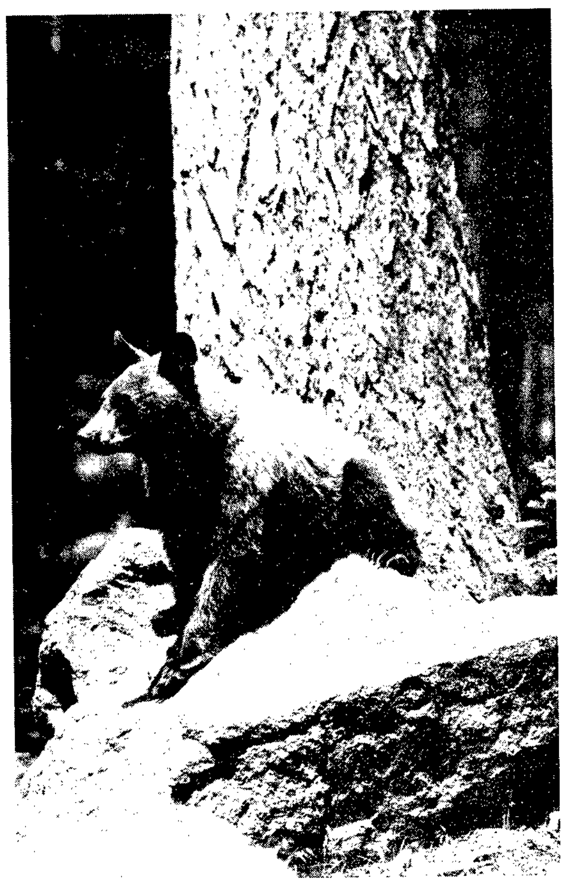

Figure 87. Black bears (Ursus americanus) and many other large mammals are direct consumers of wetland plants. (U.S. Fish and Wildlife Service photo by E. P. Haddon.)

Moose (Alces alces) are rarely encumbered by snow depths. They feed on aquatic vegetation in ponds and browse on willow in littoral zones of both streams and ponds (Figure 88). Moose seem to require a lower average daily temperature than other grazers. They are believed to escape from insect pests by submerging in ponds and lakes. They are found at high elevations at the latitude of Wyoming, but never so high as to remove them from proximity of small ponds (Denniston 1956).

As in all ecosystems, predation in wetlands occurs at several trophic levels. Aquatic invertebrates including zooplanktors, nematode and oligochaete worms, molluscs (Figure 89), crustaceans (Figure 90), and insects are an essential food source for waterfowl, insectivorous song birds, swallows, nighthawks, and foraging and game fishes. Brooding female ducks rely on this animal protein source for egg production and ducklings require it for growth. Young ducks hatch during periods of highest insect emergence (Clark 1979). Other avian predators include the endangered American peregrine falcon (Falco peregrinus anatum) and bald eagle (Haliaeetus leucocephalus).

The voracious short-tailed weasel (Mustela erminea) was the most abundant of 19 small mammal species caught on a Glacier National Park floodplain. Mink (Mustela vison) and river otter (Lutra canadensis) were consistently limited to stream and river banks (Key 1979). The endangered gray wolf (Canis lupus) and threatened grizzly bear are occasional predators in Rocky Mountain wetlands. Greenback cutthroat trout (Salmo clarki stomias) and Lahontan cutthroat trout (Salmo clark kenshawi) are endangered species, dependent for their survival upon invertebrate food sources in remote, pristine, subalpine streams.

Figure 88. Moose (Alces alces) feed on aquatic vegetation in ponds and browse on willows in carrs. (Photo by B. E. Willard.)

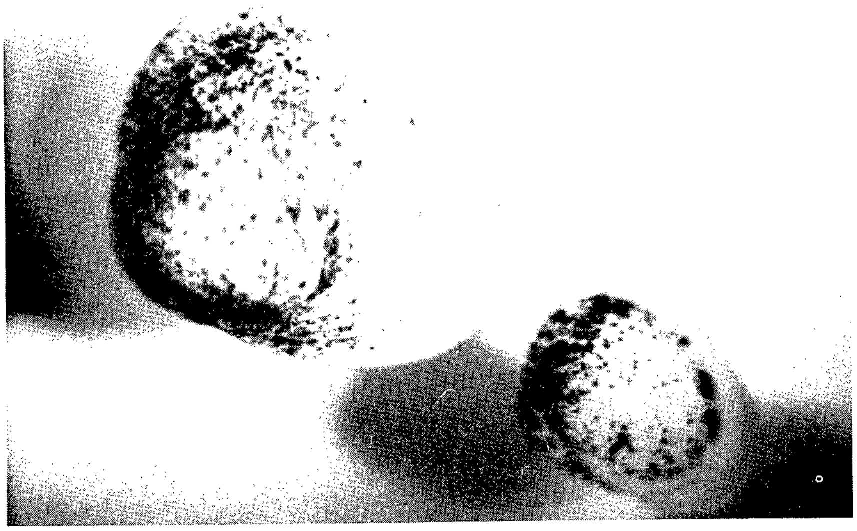

Figure 89. Fingernail clams (Pisidium sp.) are molluscs commonly found in wetlands. (Photo by J. Bushnell.)

Figure 90. Aquatic invertebrates such as the scud or sideswimmer (Gammarus lacustris) are essential food sources for waterfowl and forage and game fishes. (Photo by J. Bushnell.)

Detritus and organic leachates are utilized by bacteria, fungi, protozoans, and many larger invertebrates. Worms and many insect larvae living in wetland sediments ingest decaying plant matter. In doing so, they recycle nutrients and physically modify their environment, mixing and aerating it and allowing it to support more diverse and abundant organisms. Fecal remains or castings of these detritus feeders contain unused carbon and nitrogen compounds, which nourish other organisms ingesting them (Clark 1979). The exportation of detritus from wetlands to streams is an important contribution to the energy and nutrient budget of these ecosystems (Fisher and Likens 1973; Cummins 1973, 1974, 1976, 1977; Ward 1985).

Wetlands are essential as nurseries for four orders of aquatic insects (Ephemeroptera, Plecoptera, Trichoptera, Odonata) whose larvae or nymphs mature underwater. Some species of six other insect orders (Collembola, Coleoptera, Diptera, Hemiptera, Megaloptera, Lepidoptera) utilize aquatic habitats for rearing young (Pennak 1978; Merritt and Cummins 1984; Ward 1985). Wetlands export juveniles of these insects when they emerge (Figure 91). Fish fry and young birds may also depart after hatching, feeding, and maturing on wetland nutrients. Many aquatic insects spend their entire life cycles underwater. They may be disseminated in resistant forms on feet, feathers, fins, or fur of migrating mammals, fish, birds, and other insects.

b. Resource utilization patterns. Animals use wetland resources for food, nontrophic functions, and opportunities. The latter includes spatial utilization, such as breeding sites and nursery areas (partially discussed above), resting areas, refuge from predators, and flight staging areas. This also involved temporal utilization patterns. Migratory species utilize different wetland resources during different seasons (Figure 92). Some permanent wetland residents utilize different wetland resources annually as they proceed through their life cycles.

Figure 91. Wetlands export animal biomass to adjacent ecosystems. Here, stonefly adults whose larvae matured underwater dry wings before taking flight. (Photo by J. Windell.)

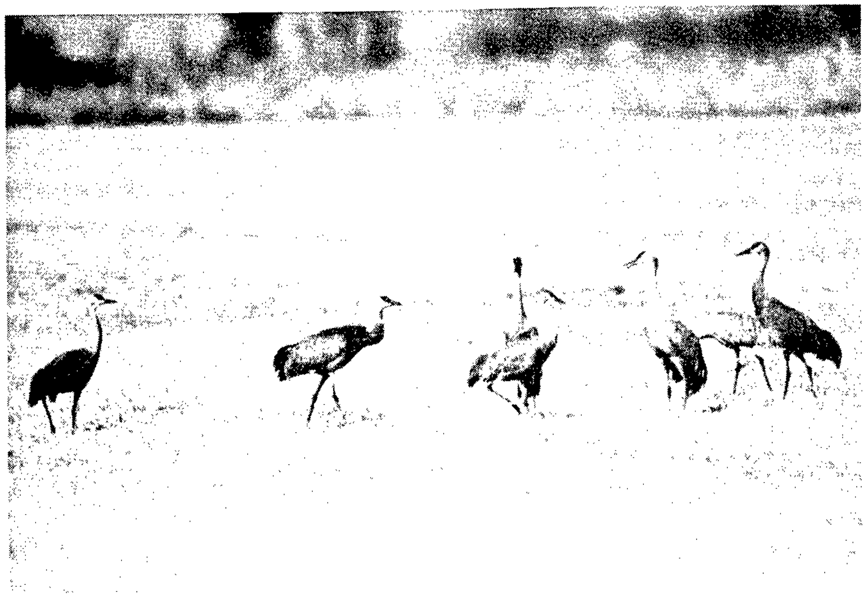

Figure 92. Migrating bird species, such as the sandhill crane (Grus canadensis), make seasonal use of Rocky Mountain wetlands for feeding, breeding sites, nursery areas, resting areas, or flight staging. (U.S. Fish and Wildlife Service photo.)

Rocky Mountain wetlands form continuous bands along streams and rivers or isolated patches in poorly drained basins, ponds, and lakes. Wetland plant species are distributed along moisture gradients (Bierly 1972), resulting in banded or clustered distributional patterns. These patterns create a high edge-to-area ratio (Odum 1978) and many ecotones with contrasting environmental factors and diverse habitats for animals. Mixed emergent or a combination of mixed emergent and submergent vegetation are most productive habitats for insects. Diverse emergent and shrubby plant species distributed in different vegetational zones are most favorable to birds and mammals.

Rocky Mountain floodplains and wetlands have highest avifauna species richness and density in habitats with mature hydric shrub cover and complex plant species composition (Wright et al. 1983; Hallock 1985). Willow carrs of the Colorado Front Range are valuable nesting sites of Wilson warblers and Lincoln sparrows. They also support maximum numbers of song sparrows and yellow warblers. The mountain riparian zone is a favorite habitat for fox sparrows, nighthawks, violet-green (Tachycineta thalassima) and tree (Iridoprocne bicolor) swallows, water ouzels (Cinclus mexicanus), red-tailed hawks (Buteo jamaicensis), and other accipiters (Hallock 1985; Knopf 1985). Riparian areas are preferred nesting sites for one quarter of bird species breeding in Wyoming (Clark and Dorn 1981). White-tailed ptarmigan utilize subalpine willow carrs during the winter months (Braun 1969; Braun et al. 1976; Hallock 1985). Coots (Fulica americana) are common breeders in ponds and backwaters (Gorenzel et al. 1982).

Beaver, oxbow, and moraine ponds and stream backwaters are nesting, feeding, and resting sites for migrating waterfowl, notably, mallards (Anas platyrhychos), green-winged teal (Anas crecca), pintail (Anas acuta), wood duck (Aix sponsa), and Canada geese (Branta canadensis). Of particular interest is the uncommon and localized occurrence of harlequin ducks (Histrionicus historonicus), in Glacier National Park. Up to 90% of their habitat use is in rushing mountain streams. Females brood on meanders and backwaters, often returning with the same mate to the same creek each year. They are extremely intolerant of human disturbance. Inland breeding of this species is rare and dependent upon access to remote natural streams and wetlands (Kuchel 1977).

Great blue heron (Ardea herodias) are colonial nesters that utilize mature cottonwood groves containing tall, robust trees with dense, broad canopies. These stands are becoming uncommon in the Rocky Mountains (Butterfield and Wright 1983).

Winter range of the endangered bald eagle (Haliaeetus leucocephalus) (Figure 93) extends throughout high desert and riverine wetlands of the Rocky Mountain region. They are occasionally observed perched on large branches in cottonwoods or conifers adjacent to rivers. In autumn, they congregate in communal roosts in Glacier National Park to feed on spawning kokanee salmon. The possible collapse of the exotic kokanee salmon population poses a potential threat to eagles. Young eagles are especially at risk, because they are unable to compete with mature eagles for live fish. Consumption of fish carcasses in large quantities during fall congregations in the park insures that they will be strong enough to continue migration and survive the winter (Shea 1978; McClelland 1973, 1981).

The whooping crane (Grus americana) is an endangered species with critical habitat in marshy and swampy wetlands and grain fields near water. Efforts are being made to re-establish breeding populations in the Rocky Mountain region by removing whooping crane eggs from nests in Canadian Northwest Territories and introducing them to sandhill crane nests in Idaho (Clark and Dorn 1981).

Migratory bird species, their nests, and eggs are protected by the Migratory Bird Conservation Act (16 U.S.C. 703, 50 C.F.R. 20.71) and the Endangered Species Preservation Act of 1972 and 1973, but habitat is not. Wetland habitat within and beyond the Rocky Mountain region deserves special attention to insure the preservation of adequate breeding, feeding, resting, and migratory staging areas for migratory bird species (Clark and Dorn 1981).

The cutthroat trout (Salmo clarki) was once native to small headwater streams throughout the Rocky Mountains. Many subspecies of cutthroat trout evolved (Behnke 1968, Behnke and Zarn 1976). Two prime causes have been responsible for the decline and disappearance of cutthroat trout from its historical range: (1) disruption or destruction of habitat by irrigation, timbering, mining, and pollution; and (2) interbreeding and competition with introduced species, such as rainbow trout, eastern brook trout, and non-native subspecies of cutthroat trout (Windell and Foster 1982). Greenback cutthroat

Figure 93. Winter range of the endangered bald eagle (*Haliaeetus leucocephalus*) extends throughout high desert and riverine wetlands of the Rocky Mountain region. (U.S. Fish and Wildlife Service photo by Don Pfitzer.)

trout (*Salmo clarki stomias*) are known to remain in genetically pure populations in only 20 miles of stream in Colorado (Stuber 1985). Cutthroat trout are on Federal and State Threatened and Endangered Species lists in Colorado (*Salmo clarki stomias*) and in Utah (*Salmo clarki henshawi*). Maintenance of wild, pure populations is considered important as a source of biotic genetic heterogeneity, and as gametes used to strengthen hatchery stock (Behnke 1968; Behnke and Zarn 1976; Stuber 1985). State wildlife divisions and the U.S. Forest Service are cooperating in efforts to identify isolated wild cutthroat populations and to improve their habitat (Stuber 1985).

Beaver create new wetlands by construction of dams. Linked beaver dams in various successional stages are common in many upper montane and lower subalpine valleys. They provide heterogeneous habitat conditions for many animal species (Grasse 1951). Before settlement of the Rocky Mountain region, beaver were, no doubt, the most influential natural force shaping wetlands.

Threatened and endangered species values. The World Wildlife Fund stated recently that the present world rate of extinction is one species per day. This figure will reach one species per hour somewhere between 1990 and 2000 (Clark and Dorn 1981). Habitat is one of the critical features for survival of any species, especially those that are low in population numbers and biological rigor.

Loss or degradation of wetlands destroys populations of plants and animals. The resulting reduction in genetic diversity and adaptability of rare survivors threatens them with extinction. People enjoy seeing unusual animals and plants. Loss of species represents loss of human values and a deprivation to present and future generations of resources created over millions of years of evolution (Darnell 1979).

The U.S. Fish and Wildlife Service is mandated by the Threatened and Endangered Species Acts of 1972 and 1973 to list threatened and endangered species of wildlife and plants.. It is important to recognize that there are plant and animal species with critically small populations or limited distribution that have not yet received Federal designation. Some of these are protected locally by State rare and endangered designations. Plants and animals of the Rocky Mountains with Federal Threatened or Endangered Status are listed in Table 37.

Wildlife refuge values. The U.S. Fish and Wildlife Service administers a network of National Wildlife Refuges and Wetland Management Districts that have been established by Acts of Congress, primarily in the interest of protecting migratory birds and waterfowl. Refuges in the Rocky Montain region represent a diverse combination of open water, wetlands, river bottoms, and prairie uplands required for birds migrating along the Central and Pacific flyways (Figure 94). Many were established in the interest of protecting habitat essential to migrating whooping cranes and trumpeter swans (Chadwick 1985).

Private nonprofit organizations have also worked for perpetuation of wildlife species and the unique lands that they inhabit. The Nature Conservancy has contributed 50% of its funding to preserving wetlands. The National Audubon Society owns or leases 70,986 ha (175,273 ac) of wetlands. Other groups interested in lobbying for wetland protection include Sierra Club, National Wildlife Federation, Ducks Unlimited, Trout Unlimited, and various local conservation groups. The U.S. Fish and Wildlife Service works with many of these organizations to identify additional wetland habitat for future Wildlife Refuge designation.

There is a need to assess the effects of even limited human activity within some National Wildlife Refuges. In Redrocks Lake National Wildlife Refuge, Montana, nesting waterfowl continue to be disturbed by canoeists, fishermen supported by floatation rings, and hunters that have been given special permission to use motorboats (Chadwick 1985).

Table 37. Federally listed Endangered and Threatened Species and Proposed Species in Region 6 of the U.S. Fish and Wildlife Service as of February, 1985. U.S. Department of the Interior (1984).

Colorado

Mammals:	Black-footed ferret (Mustela nigripes)
Birds:	W American peregrine falcon (Falco peregrinus anatum)
	W Arctic peregrine falcon (T) (Falco peregrinus tundrius)*
	W Bald eagle (Haliaeetus leucocephalus)
	W Eskimo curlew (Numenius borealis)**
	W Interior least tern (P,E) (Sterna antillarum athalassos)
	W Whooping crane (Grus americana)
Fish:	W Bonytail chub (Gila elegans)
	W Colorado squawfish (Ptychocheilus lucius)
	W Greenback cutthroat (T) (Salmo clarki stomias)
	W Humpback chub (Gila cypha)
Plants:	Clay-loving wild buckwheat (Eriogonum pelinophilum)
	Knowlton's hedgehog cactus (Pediocactus knowltonii)
	Mancos milk-vetch (P,E) (Astragalus humilimus)
	Mesa Verde cactus (T) (Sclerocactus mesae-verdae)
	North Park phacelia (Phacelia formosula)
	Spineless hedgehog cactus (Echinocereus triglochidiatus var. inermis)
	Uinta Basin hookless cactus (T) (Sclerocactus glaucus)

Wyoming

Mammals:	Black-footed ferret (Mustela nigripes)
	Gray wolf (Canis lupus)
	W Grizzly bear (T) (Ursus arctos horribilits)
Birds:	W American peregrine falcon (Falco peregrinus anatum)*
	W Arctic peregrine falcon (T) (Falco peregrinus tundrius)
	W Bald eagle ((Haliaėetus leucocephalus)
	W Eskimo curlew (Numenius borealis)**
	W Whooping crane (Grus americana)
Fish:	W Kendall Warm Springs dace (Rhinichthys osculus thermalis)
Amphibians:	W Wyoming toad (Bufo hemiophrpys baxteri)

Table 37. (Concluded)

Utah		
Mammals:		Black-footed ferret (<u>Mustela</u> <u>nigripes</u>)
		Utah prairie dog (T) (<u>Cynomys</u> <u>parvidens</u>)
Birds:	W	American peregrine falcon (<u>Falco</u> <u>peregrinus</u> <u>anatum</u>)
	W	Arctic peregrine falcon (T) (<u>Falco</u> <u>peregrinus</u> <u>tundrius</u>)*
	W	Bald eagle (<u>Haliaeetus</u> <u>leucocephalus</u>)
	W	Eskimo curlew (<u>Numenius</u> <u>borealis</u>)**
	W	Whooping crane (<u>Grus</u> <u>americana</u>)
Montana		
Mammals:		Black-footed ferret (<u>Mustela</u> <u>nigripes</u>)
		Gray wolf (<u>Canis</u> <u>lupus</u>)
	W	Grizzly bear (T) (<u>Ursus</u> <u>arctos</u> <u>horribilis</u>)
Birds:	W	American peregrine falcon (<u>Falco</u> <u>peregrinus</u> <u>anatum</u>)
	W	Arctic peregrine falcon (T) (<u>Falco</u> <u>peregrinus</u> <u>tundrius</u>)*
	W	Bald eagle (<u>Haliaeetus</u> <u>leucocephalus</u>)
	W	Eskimo curlew (<u>Numenius</u> <u>borealis</u>)**
	W	Interior least tern (P,E) (<u>Sterna</u> <u>antillarum</u> <u>athalassos</u>)
	W	Piping plover (P,T) (<u>Charadrius</u> <u>melodus</u>)
	W	Whooping crane (<u>Grus</u> <u>americana</u>)

(T) = threatened; (P,T) = proposed as threatened; (P,E) = proposed as endangered; all other endangered; W = dependent upon wetland at some time in life cycle.

*The Arctic peregrine falcon is considered endangered when migrating through the lower 48 states because of its similarity and appearance to the American peregrine falcon.

**The Eskimo curlew formerly migrated through the Great Plains area in the spring, but none have been seen in this area for many years. Recent sightings are all from the Gulf Coast, Caribbean area, and Canada.

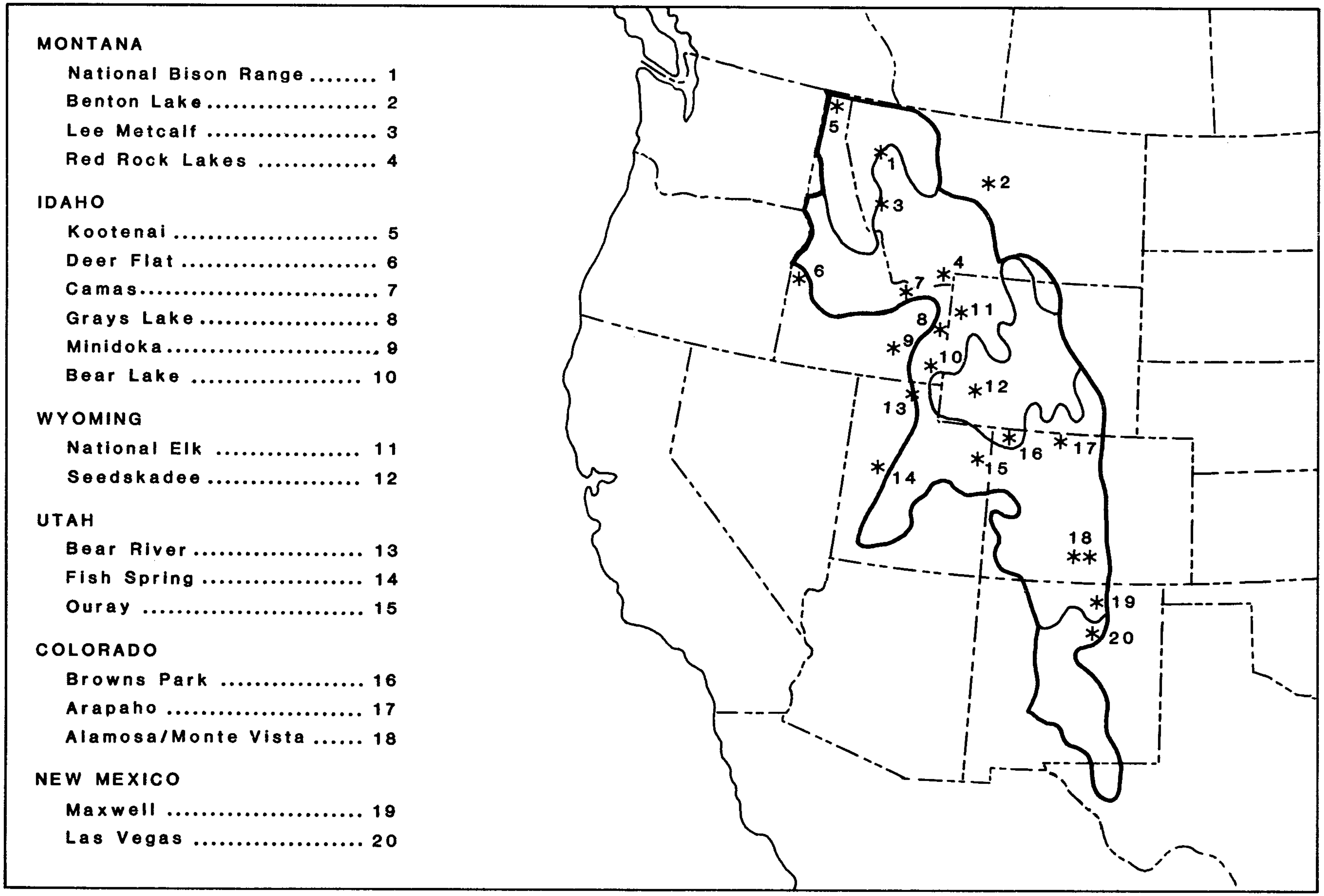

Figure 94. Locations of National Wildlife Refuges in the Rocky Mountain region.

Experiential Values

Experiential values are the worth attributed to wetlands by human direct sensory experience. In this case, there is no substitute for being there; one cannot "experience" wetlands second hand. Experiential benefits from wetlands may be ethical, spiritual, physical, aesthetic, and recreational (Figure 95). For centuries, poets, writers, musicians, theologians, philosophers, and artists have sought inspiration from them. Wetlands are a part of human cultural heritage (Odum and Odum 1972; Fritzell 1979; Niering 1979; Reimold and Hardisky 1979; Smarlson 1979).

Wetlands provide scenic variety and an attractive edge to the land-water interface that is noticed at a glance. Lush green foliage with soft textures contrast with open water, upland vegetation, and exposed geological features. Wetlands form a buffer between waterways and commercial, residential, and agricultural lands. They provide lowland open space in the Rockies between rugged, densely forested mountainsides. When wetlands are viewed from above, zones of wetland plants adapted to different hydrological environments create intriguing patterns, enticing the observer to reflect on the history, future, unique processes, and intrinsic beauty of these ecosystems (Figures 34, 41, and 61).

Figure 95. Experiential benefits may be ethical, spiritual, physical, aesthetic, and recreational. (Photo by B. Foster.)

Nature lovers are drawn to wetlands. Their growing season is a spectacular procession of floral displays. Ospreys (Pandion haliaetus), eagles, waterfowl, and small nesting birds are attracted to productive open waters and protective stands of shrubs, trees, and emergent plants. At dawn or dusk, a careful observer is serenaded by bird song and transfixed by a passing beaver, muskrat, bear, moose, or elk. Preserved in their natural state, wetlands provide a lure of wilderness to many people, who are renewed and nurtured by experiencing them and knowing that they continue to exist.

Recreational experiences in wetlands offer the sportsperson contrast from office and home environment, and opportunities to enhance physical fitness and self-knowledge by pushing back physical and psychological limits previously considered permanent barriers to growth.

Outdoor enthusiasts value wetlands as sites for recreational nature study, photography, boating, skating, skiing, fishing, hunting, and hiking. Over $307 million were spent on food, drink, transportation, guide fees, pack trips or package fees, land-use fees, and equipment rental for nonconsumptive wildlife use in the Rocky Mountain States in 1980 (U.S. Department of the Interior 1982).

Consumptive recreational activities are also popular in wetlands. Nearly a million individuals were licensed to hunt elk, black bear, mule deer, and moose and nearly two and a half million individuals purchased licenses to fish in the Rocky Mountain States (U.S. Department of the Interior 1982). Beaver, otter, raccoon, skunk, and weasel were also trapped for their fur value (Office of Technology Assessment 1984).

Vast acreages of public lands are regulated by multiple-use management policies. They provide a wealth of opportunities for outdoor experiences enjoyed by millions of visitors each year. Consumptive recreational usership can be determined to a certain degree of accuracy by licensing and expenditure data. It is more difficult to assess the effects of management alternatives on the aesthetic attributes of the land. Means of assessing forest scenic beauty are reviewed by Brown and Daniel (1984). An assessment model is described and its utility evaluated. This and other models discussed may be useful in determining aesthetic value of wetlands in the Rocky Mountain region. Assignment of economic value to nonmarketable on-site wetland uses is another method for evaluating the importance of aesthetic experiences.

Educational and Scientific Values

Wetlands are outdoor laboratories for students and scientists in fields of botany, ornithology, aquatic ecology, mammology, entomology, evolution, genetics, chemistry, and soil science. They are complex natural ecosystems in which all species have evolved to play an integral role in natural processes and to contribute to the overall order and stability of the ecosystem. Scientific endeavor in this medium is worthwhile, simply for the satisfaction derived from it. Science also reveals how things work, how they used to be, and how they can be used (Rolston 1981).

Educational programs and scientific research in wetland ecology are of critial importance due to the threatened status of wetlands. Unspoiled wetlands provide important baseline information and serve as models for restoration of those that have been impaired. They contain plants and animals that may at some time provide society with food, useful chemicals, and services. The public and decisionmakers must know more about wetland structure, function, and unique attributes in order to promote wise stewardship of remaining wetland areas.

Educational opportunities in or tangential to wetlands are available through ecology, biology, and natural resources departments of State universities in the Rocky Mountain region (Figure 96). They are also provided by private organizations such as the Aspen Center for Environmental Studies (Aspen, Colorado), Teton Science School (Jackson, Wyoming), Cloud Ridge Naturalists (Ward, Colorado), Rocky Mountain Nature Association (Estes Park, Colorado), Audubon Science Camp (Dubois, Wyoming), and Denver Museum of Natural History, to name a few. National Parks employ well-trained naturalist interpreters that lead field trips and classes in wetlands. Several Rocky Mountain Wildlife Refuges and wetland-based environmental education centers, such as the Aspen Center for Environmental Studies, provide self-guided tours of wetlands. Before designing an interpretive program in a wetland, it is wise to conduct a systematic plan for development of facilities and programs (Chapman 1974). This will insure an efficient and effective use of the wetland while protecting it from damage due to human activities.

Figure 96. Key components and processes of a wetland food chain dramatized by elementary school students on a field trip to river bottomland at Aspen Center for Environmental Studies, Colorado. (Photo by S. Foster.)

Economic Values

An economic value is (1) a good, service, or amenity that provides at least some consumers (not necessarily all) with satisfaction or enjoyment; and (2) scarce enough so that consumers demand more than is available (Loomis et al. 1985). Although fish and wildlife meet these two criteria, they have not traditionally been recognized in economic analyses of natural lands.

Several factors are forcing managers of public lands and private interest groups to assess the economic value of nonmarketable ecological goods and services. The Resources Planning Act, Flood Control Act, National Environmental Policy Act of 1969, Executive Order 12,291, and National Forest Planning Act require explicit consideration of economic benefits, costs, and impacts of policy changes with regard to wildland resources. Amendments to the Endangered Species Acts of 1972 and 1973 permit exemptions when economic arguments for the exemptions are strong (Peterson and Randall 1984). It is also argued that only when fish, wildlife, and natural amenities are adequately assigned economic worth will they be given full recognition in competition with marketable natural land uses, such as timber sales, livestock grazing, and minerals extraction (Salwasser et al. 1984).

This discussion summarizes studies relevant to economic valuation of Rocky Mountain wetlands. A review of general economic theory, current valuation methods, and terminology pertinent to identification of economic value of nonmarketable natural goods and services is provided in Appendix C.

The economic value of various features of southeastern tidal salt marshes was determined by Gosselink et al. (1973). They analyzed four categories of monetary values:

(1) by-product production (fisheries, nutrient contribution to adjacent ocean, etc.),

(2) potential for aquaculture development,

(3) waste assimilation, and

(4) total "life support" values as a function of primary production.

Economic value of oyster production (Batie and Wilson 1978) and more general benefit values (Silberhorn et al. 1974) have been determined for Virginia coastal wetlands. A benefit model has also been proposed for a freshwater wetland in Massachusetts (Gupta and Foster 1975). At the time, these studies were a great advance in wetland valuation in that they selected unique sets of public benefits from wetlands and suggested individual approaches to assessing them. They did not consider valuation of offsite nonconsumptive uses (existence, option, and bequest values) for which, we now know, people are willing to pay.

Several studies have addressed economic value of resources completely or partially dependent on Rocky Mountain wetlands. One study determined appropriate assessment methods and values associated with wild trout fishing in Idaho (Sorg and Loomis 1984). Also in Idaho, average willingness to pay

has been determined for steelhead fishing, in theoretical values acceptable to several Federal agencies and the State (Sorg et al. 1984; Donnelley et al. 1985b). A review of empirical studies published since the 1960's evaluates net values of hunting and fishing (Table 38), wild trout and cold-water fishing (Table 39), camping fees (Table 40), and ranges of average willingness to pay for a variety of recreational opportunities (Table 41). These studies were conducted throughout the western mountain, intermountain, and northwestern States (Peterson 1985).

Two studies are relevant to determining fees assessed for wetland recreational use. Rosenthal et al. (1984) discussed alternative pricing systems for publicly provided recreational opportunities in wilderness, rivers, lakes, and reservoirs, for dispersed recreation (e.g., hiking, backpacking, crosscountry skiing), and for urban parks. The other study describes past and future trends in user fees (Driver et al., in press).

Several recent studies have concluded that when considering unique species or habitats, the public is much more willing to pay for nonconsumptive uses (option, bequest, and existent off-site values) than for consumptive uses (recreation and commercail on-site values). Recreation use value and public preservation value of endangered Colorado wildlife species were determined by randomly sampling 198 households using the contingent value method (Walsh et al. 1986). Present total value of endangered wildlife program benefits were estimated to be $838.1 million. Public preservation value ($592.9 million) was nearly three times that of recreation value ($245.4 million). Net economic value of bighorn sheep hunting in Idaho (determined by Travel Cost Method) amounted to only 1% of annual economic benefits of this species when compared with estimates of public nonconsumptive use (existence) value (Loomis 1986). Willingness of Colorado citizens to pay for off-site nonconsumptive uses of 11 potential Wild and Scenic Rivers represented 80% of total willingness to pay estimates (Walsh et al. 1986). On-site recreational use represented the other 20%. These studies stressed that Federal and State agencies should improve economic efficiency of natural resource management by including estimates of off-site nonconsumptive value in economic analyses of unique wildlife species and habitats faced with irreversible management changes.

The last decade has been a productive one for development and refinement of methods for assessing economic value of nonmarketable natural goods and services. There is a need to apply these methods to specific wetland studies and to refine them even more to serve the purpose of adequately representing wetland wildlife, plants, and ecological functions in the economic arena.

Table 38. Average daily consumer costs, willingness-to-pay (WTP), and benefits for hunting and fishing in Idaho (1982 dollars).[a]

Activity	Average daily recreationist costs	Average additional WTP per day	Average total benefit
Upland game hunting	$20.90	$28.50	$49.40
Pheasant hunting	17.99	24.44	42.43
Cold-water fishing	23.45	25.55	49.00
Warm-water fishing	18.10	26.36	44.46
Water fowl hunting	37.26	45.69	82.95
Elk hunting	26.93	35.18	62.11
Deer hunting	18.39	26.33	44.72
Steelhead fishing	46.59	14.29	60.88
Bighorn sheep hunting	-	27.80	-
Moose hunting	-	19.12	-
Antelope hunting	-	38.58	-
Mountain goat hunting	-	90.00	-

[a]Donnelley et al. 1985a. Net economic value of hunting and fishing in Idaho.

Table 39. Average net willingness-to-pay (WTP) for wild trout fishing and other cold-water fishing, 1983. (From Peterson 1985.)

Question	Wild trout	Other cold water
Trip worth more than cost (% yes)	84%	79%
Additional WTP per trip	$35.49	$27.95
WTP for 50% bigger fish	$10.17	$15.32
WTP for 50% more fish	$ 5.65	$ 9.62
Expenditures per trip	$54.08	$42.62
Fish caught per trip	7.40	5.35
Trip duration (calendar days)	1.95	1.62

Table 40. Average daily camping fees (1984 dollars). (From Peterson 1985.)[a]

Agency	1977	1978	1979	1980	1981	1982	1983	1984
U.S. Forest Service	3.64	3.44	3.21	2.93	3.31	4.23	4.55	4.58
National Park Service	-	-	-	[---3.19---]		5.06	5.42	-
Corps of Engineers	-	-	-	3.93	3.89	4.83	5.07	5.29

[a]Average willingness-to-pay (WTP) estimates for camping from Sorg and Loomis (1984), in 1984 dollars, were from $6.18 to $28.08.

Table 41. Ranges in average willingness-to-pay[a] (WTP) (1982 dollars) for a variety of activities. (From Peterson 1985.)

Activity	Number of studies	Adjusted WTP per 12-hour activity day
Anadromous fishing	6	$25.92 - 99.02
Big game hunting	15	16.81 - 131.80
Camping	10	5.80 - 26.35
Cold water fishing	15	8.58 - 67.55
Warm water fishing	5	14.85 - 26.35
Hiking	6	8.25 - 45.67
Nonemotorized boating	4	6.28 - 33.22
Picnicking	5	6.53 - 28.54
Small game hunting	4	15.74 - 42.58
Water fowl hunting	7	16.26 - 84.73
Water sports	5	10.26 - 27.00
Wilderness	5	12.78 - 73.93

[a]From Sorg and Loomis (1985).

5.4 METHODS FOR ASSESSING WETLAND FUNCTIONS AND VALUES

An immense field lies open for research in assessment of functions and values of Rocky Mountain wetlands. No assessment model has been developed and applied to these ecosystems. One recent publication reviews the literature of wetland evaluation methodologies (Environmental Protection Agency 1984). This document would be of interest to a person considering development or adaptation of an assessment model to the region's wetlands. No consistent evaluation method is being employed by government agencies or private interests managing Rocky Mountain wetlands.

The Federal Highway Administration (FHWA) has gone to some length to develop and review a functional assessment model (Adamus 1983; Adamus and Stockwell 1983). The model underwent thorough review by a group of ecologists well known for their expertise in North American wetland ecology (Sather and Stuber 1984). Recommendations from the review have not been incorporated into the model at this time, but a publication summarizing recommendations (Sather and Smith 1984) is suggested as a companion to the model. The FHWS Assessment model is, of course, especially sensitive to impacts on wetlands by highway construction activities. Rink (pers. comm.) applied it in a study of a montane/subalpine wetland in Colorado. The model was difficult to use because it assumes a certain degree of wetland homogeneity not characteristic of this region. However, efforts are currently underway to develop regionalized versions of this methodology.

Assessment of wetland functions and values is of critical importance in this era of rapid and irreversible wetland alteration. It is especially critical to the field of impact assessment, since, impacts cannot be accurately predicted without profound understanding of wetland structure, functions, and values.

CHAPTER 6

IMPACTS TO WETLANDS AND IMPLICATIONS FOR MANAGEMENT OF ROCKY MOUNTAIN WETLANDS[1]

6.1 INTRODUCTION

Historically, until fairly recently, Rocky Mountain wetlands were regarded as waste areas; their natural values and functions went largely unrecognized. No one questioned the European immigrant wisdom of converting as much as possible of one's "wasted" wetland acreage into useful cropland. Even George Washington, in 1763, was on a survey group for draining wetlands for conversion to agricultural purposes. Extremely ambitious drainage projects followed in Delaware, Maryland, New Jersey, Massachusetts, South Carolina, and Georgia. Drainage ditches and clay tile pipe became standard engineering practices for draining wetlands as early as 1835. By 1880, there were 1,140 tile factories in the United States, most of which were located in Illinois, Indiana, and Ohio.

Historically, the Federal Government encouraged and offered large financial inducements to wetland development projects. A number of favorable laws and subsidies further encouraged development of wetlands for agriculture in the 19th century. The Swamp Land Acts of 1849, 1859, and 1860 gave 65 million acres of wetlands owned by the Federal Government to 15 States for conversion to agricultural dry land. During the 1930's, the Federal Governments's role in land drainage was accelerated through the emergency public works programs. As late as 1953, the Department of Agriculture, through the Soil Conservation Service, announced that 50 million acres of wet swamp lands that were subject to overflowing "...would be physically suitable for crop or pasture use" if drainage measures were employed (Wooten 1953).

Although the environmental destruction of wetlands has continued up to the present, it has been significantly decreased as a result of a major governmental policy shift in the use of wetlands. By 1975, the Soil Conservation Service issued a Conservation Planning Memorandum indicating a nearly complete reversal in its earlier position. The memorandum indicated that, regarding 18 of the 20 types of wetlands described in the 1954 Fish and Wildlife Service Survey, the Soil Conservation Service was not to provide technical and financial assistance for drainage or otherwise altering wetland " ... in order to convert them to other land uses." It was further indicated that millions of acres of the Nation's original wetlands were impaired or converted to other uses and that extraordinary care and effort would be required to protect the remaining wetland ecosystems.

[1]Authored by J. T. Windell.

In the United States, total natural wetlands have been estimated at 51,435,000 ha (127,000,000 ac), of which about 18,225,000 ha (45,000,000 ac), or 35%, were drained or converted by 1950 (Shaw and Fredine 1956). Although it is difficult to evaluate the accuracy of these drainage figures, some authors have estimated that at least 50% of the Nation's wetlands have been drained or destroyed. Likewise, little information is available for the Rocky Mountain Province. Reports strongly suggest that drainage continues to occur in spite of protective legislation. One estimate puts the National yearly loss of wetlands at 121,500 ha (300,000 ac) (United States Department of Agriculture 1980).

6.2 LOSSES OF RIPARIAN WETLAND HABITAT

Historically, riparian wetland habitats were frequently the first areas settled by European immigrants. Rocky Mountain riparian wetland ecosystems and fertile valley floodplains provided an abudance of game, fish, and other easily harvestable natural resources needed by settlers until they could bring lands into production. Many water courses provided the only means of transporting large quantities of supplies and goods. Water power was harnessed to grind grain, saw wood, and accomplish many other needed tasks. The same fertile, alluvial, and wetland soils that provided excellent wildlife habitat also provided excellent farmlands after they were cleared of dense stands of riparian and wetland vegetation, and drained. Water from these riparian wetland ecosystems commonly was used to irrigate croplands. Trees were cut for firewood, timber, or both (Sands 1980).

The major disadvantage experienced from living within the riparian wetland areas was the frequent flooding of farms, villages, and crops. Early settlers, however, were willing to accept and adapt to the flooding inconveniences in order to capitalize on the many assets that the riparian wetland and floodplain areas offered.

Numerous studies (Thomas et al. 1979; Warner 1979, 1980) have reported that riparian wetland habitat types (on a worldwide basis) are disproportionately more important for support of wildlife and concentrated human activity than any other type of ecological habitat. Rocky Mountain riparian wetland habitat is no exception and is especially vulnerable to impact in the narrow mountain valleys. The unfortunate result of concentrated human activity within the Rocky Mountain riparian wetland habitat is its wholesale destruction. Some authors have been prompted to declare this habitat "threatened" and in danger of becoming "extinct." Recent reported estimates indicated that 70% to 90% of the natural riparian wetland habitat in the United States has been lost to human activities (Council on Environmental Quality 1978; Warner 1979; Swift and Barclay 1980; Swift 1984).

This crisis of riparian wetland ecosystem degradation has been recognized by Federal agencies that have issued position papers, directives, and sponsored National symposia concerned with protection, maintenance, and enhancement of riparian wetlands (Almand and Krohn 1978; Hirsch and Segelquist 1978; Benson 1979; U.S. Department of the Interior, Bureau of Land Management 1979b; Warner 1979; McCorkle and Halver 1982). The Council on Environmental Quality (1978) stated in its ninth annual report that "no ecosystem is more essential than the riparian to the well-being of the Nation's fish and wildlife."

The significance of riparian wetland habitat degradation can be easily understood when one considers that riparian habitat is an extremely limited and finite resource, making up only a tiny fraction of the total landscape (Johnson and Jones 1977). Data from the U.S. Forest Service and the Bureau of Land Management serve best to illustrate: of the 173 million acres managed by the Bureau of Land Management and the 76 million ha (187 million ac) managed by the Forest Service in the Western United States (excluding Alaska and Hawaii), much of which is in the Rocky Mountain Province, only 0.3% or 210,195 ha (519,000 ac) and 1.2%, 909,630 ha (2,246,000 ac), respectively, are composed of riparian wetland ecosystems (Cope 1979). In addition, Bureau of Land Management administrators have reported that 83% or 174,555 ha (431,000 ac) of their publicly owned riparian wetlands in the West (excluding Alaska) are in an unsatisfactory condition (Almand and Krohn 1978), leaving only 35,640 ha (88,000 ac) (17%) in satisfactory condition.

Losses of riparian wetland habitat and associated wildlife have been most dramatic in the West and Midwest because of the relative scarcity of these habitat types and the intense demand man has placed on the water and land resources of these regions. An estimated 90% to 95% of the cottonwood-willow habitat of the lower foothills (montane) and high plains of the Rocky Mountain West has been lost (Beidleman 1978; Johnson and Carothers 1980). Cottonwood communities along the Colorado River have declined from an estimated 2,025 ha (5,000 ac) to only about 202 ha (500 ac) as a result of changing hydrologic regimes resulting from upstream dams and reservoirs. There are still some 1,134 ha (2,800 ac) of willow-cottonwood stands along the river, but most are invaded by salt cedar, an exotic introduction of much lower value to wildlife and a much higher consumer of water.

As Rocky Mountain development continues, people are looking for ways to increase water supplies for agricultural, industrial, and urban uses; to increase crop production; and to protect crops, homes, and industries from flooding. Many combinations of draining, diking, diverting, leveeing, damming, and channeling continue to be used to accomplish these goals. Even with increasing legal protections, additional clearing, conversion, and alteration of natural riparian wetland habitat continues at a steady but piecemeal pace. Development, water diversions, dams, reservoir construction, overgrazing, and numerous other human activities continue to eat away at the remaining linear mileage of riparian wetland habitat types. No large-scale systematic quantification of riparian wetland habitat (or the amount of man-caused alteration) has been reported for the Rocky Mountains or the Nation.

6.3 WETLAND ORIGIN AND CREATION

All wetlands have been created either by natural processes or by human activities. Principal natural processes responsible for wetland origin include: (1) depressions left by glaciers, (2) inundation of wave-protected coastal lowlands, (3) erosion and deposition by rivers, (4) beaver dams, and (5) miscellaneous processes, such as earthquakes, soil deposition by wind, and formation of sink holes. Human activities responsible for wetland creation include: (1) construction of ponds, reservoirs, and borrow pits, (2) water stabilization measures on lakes, (3) gravel mining within flood plains and the formation of gravel pit ponds, (4) obstruction of natural drainages by levees, fills, road, and railroads, and (5) leaky irrigation systems.

Historically, wetland creation by human activities went largely unrecognized. Recent public and government concern about wetland habitat losses, however, has prompted Rocky Mountain land managers and others to recognize many benefits from intentional creation of wetlands. Several techniques have received consideration, including annual flood irrigation, lowering land surface areas to near the existing water table, and lowering or contouring land surfaces to create saturated soil conditions. In each case, these types of areas are seeded with native wetland plants from impacted areas or irrigation ditches.

Most of these intentionally created wetlands are a direct result of mitigation agreements that require wetland replacement for wetland impacted or lost because of development (Swanson 1979). However, the created wetlands may show little structural and functional relationship to lost natural wetlands, which is of major concern to land managers.

6.4 IMPACTS TO ROCKY MOUNTAIN WETLANDS

The impacts of human activities on Rocky Mountain wetlands are many and long lasting. Although an unknown amount of wetland acreage has been created by various human activities, significant acreages have been negatively impacted. Much of the impact is a result of population concentration within selected Rocky Mountain areas. For example, population tends to be sparse within the high plains regions, heavy along the junction between the plains and the mountains, and moderate in the mountains along narrow valley floodplain corridors. Observation indicates that development is concentrated along watercourses, which receive the greatest cumulative wetland habitat modification and losses. A discussion of some major perturbations occurring within the often narrow floodplain valleys follows.

Recreation and Other Development

The major adverse impacts to Rocky Mountain wetlands are a direct result of ongoing dredge and fill for development and related human activities. In the Rocky Mountains, many developmental activities are related to recreation, especially skiing, vacation houses, and other resort facilities. These recreational developments often include drainage of wetland riparian areas and filling for buildings and parking areas. Although few of these projects affect significantly large acreages of any one watershed, the cumulative effect of many small wetland habitat modifications is of primary concern. Panek (1979) voiced concern for the existing piecemeal analysis of environmental impacts and the need for comprehensive evaluations of multiple impacts within a watershed and their potential cumulative effects on wetland, riparian, and aquatic communities. Of particular concern are habitat modifications associated with projects for which an environmental evaluation is not required and therefore not identified or regulated by resource management agencies (Panek 1979). It is unfortunate, but true, that only after-the-fact do we perceive the cumulative impact of numerous small wetland habitat modifications and loss of multiple resource values (Fish et al. 1966). Specifically, it is the accumulation of small habitat modifications over the long term that may pose the single greatest threat and endangerment to Rocky Mountain wetland

resources. There are literally unlimited and unknown numbers of activities impacting and affecting a finite wetland, riparian, or riverine resource. At present, no Federal bureaucracy, and no combination of Federal, State, or private agencies can possibly monitor, protect, preserve, and enhance various aspects of the wetland resource from an insidious accumulation of small modifications to habitat.

Drainage

Altering natural drainage characteristics commonly causes significant changes in wetlands. Ditching lowers the water table, which increases aeration/decomposition, increasing peat bulk density, causing a decrease in permeability and water storage capacity (Verry and Boelter 1978). Resultant impacts on vegetation can also be great. Wilson (1969) reported that Rocky Mountain wetland vegetation is very sensitive to water level. Lowering the water table by channeling, for example, turned bog peat into alpine meadow topsoil, and a spikerush community was replaced by marsh marigold. Raising the water table in an Indiana marsh shifted the plant community from *Carex* spp. to *Typha* spp. (Wilcox et al. 1985). Increasing wetness in English blanket bogs reduced seedling survival and production of vascular plants, while *Sphagnum* moss production increased (Forrest and Smith 1975).

Dewatering, Diversion, and Irrigation

Municipal and industrial water supplies, local and transmountain water diversions, and irrigated agriculture all remove water from Rocky Mountain wetland ecosystems with little regard for the short- and long-term effects. Stream diversions are commonplace in the Rocky Mountains, as are dry streambeds. Out of a total warmwater stream mileage of 11,823 km (7,348 miles) in Colorado, the Colorado Division of Wildlife reported that there were only 1,212 (753 mi) remaining kilometers of warmwater stream fishery. The original mileage was determined to be either too small, dewatered, or degraded by poor eastern plains land-use practices, or have been subjected to an unknown number of other types of habitat modifications, such as channelization. In Colorado, for example, there are 780 municipal water supply systems, 460 noncommunity (private) water supply systems, and many independent systems dependent upon deep-well water sources. Most of the water for these systems is removed from free-flowing riverine/wetland ecosystems and rapidly dropping underground aquifers. Certainly, no one can be critical of this, but consider what follows and the cumulative impacts.

Irrigated agriculture in the 17 western States accounts for 90% of the Nation's total irrigated acreage, 74% of the total water diversion, and 91% of the total water consumption. Municipal water supplies are but a drop in the bucket compared to irrigated agriculture. Much of this irrigation activity is concentrated on medium-size and large streams that only make up 12% and 3% of the total riverine and riparian wetland habitat.

Irrigated agriculture constitutes the largest single consumptive use of water in Colorado. Colorado ranks fourth Nationally, irrigating over 1,161,096 ha (2,874,000 ac). Harvested, irrigated cropland equals 42% of the total harvested cropland in Colorado.

Water is generally transferred from western slopes to eastern slopes and north slopes to south slopes through tunnels. Colorado currently has over 40 transbasin diversion systems with more being planned, designed, and constructed. All of these projects remove water from free-flowing riverine and riparian wetlands and, in many cases, result in significant dewatering and changes in the annual water regime, at least during certain periods. Some diversions return water to other systems creating unnatural "super flows." Therefore, riverine and riparian wetland ecosystems may be water-gorged or water-starved at any one point in time. To make matters worse, super flows may pose a threat to life, limb, and property and thereby generate a perceived need for channelization projects. All of this water starvation and water gorging results in habitat losses, a decreased recreational potential, and greater stress on the already stressed riverine and riparian wetland ecosystems.

Channelization

Riverine, wetland, and riparian ecosystems in the United States have been undergoing modification for more than 150 years with little or no thought that they are a finite natural resource. One of the earliest modifications occurred in 1839 when Lt. Robert E. Lee of the U.S. Army Corps of Engineers (COE) built a stone and brush dike across a chute (side channel) in the Mississippi River near St. Louis to improve the channel for navigation. Since then, stream modifications and channelization under the disguise of "channel improvement" for navigation, highway construction, flood control, agricultural development, and a host of other reasons have become major programs under the Federal Flood Control Acts of 1948 and 1960 and under the small watershed program of Public Law 566, which provided for the establishment of a National Stream Alteration Team within the U.S. Fish and Wildlife Service (USFWS) in 1975.

Although most channelization is carried out by Federal agencies, such as the Army Crops of Engineers and Soil Conservation Service (SCS), some is done concurrent with urban and industrial development and with the activities of such groups as the Farmers Home Administration, and State and local highway departments. Preparation and promulgation of channel modification guidelines by the SCS and the USFWS assist their personnel in identifying when and where channel modifications may be used as a technique for implementing water and related land resource projects. In passing Public Law 566, Congress recognized that erosion, floodwater, and sediment can cause damage in the watersheds. It is agreed that loss of life and damage to property constitute a menace to the National welfare and that the Federal Government must cooperate with States and their political subdivisions for the purposes of preventing such damages and furthering the conservation, development, utilization, and disposal of water. It was mandated that "improvements" should preserve, protect, and improve the Nation's land and water resources and the quality of the environment. It was further recognized that stream high flows and periodic overflow have a significant value in creating and maintaining meandering channels and in cleansing and redistributing substrates. This action by water provides riffles, pools, or other habitat for fish spawning and rearing, and production of aquatic invertebrates. High flow also provides diverse plant successional areas and other types of shoreline habitat that fulfill fish and wildlife food and cover requirements. It was also recognized, however, that many areas adjacent to streams and wetlands are well-suited for and have a long history of agricultural and urban uses. Therefore, channel modification

for flood control, drainage, and irrigation projects has often resulted in severe conflict with the structure and function of associated wetlands, which changes or reduces both the variety and abundance of fish and wildlife resources.

Throughout the United States, especially in the north-central regions with intensive agricultural land use, there is an ongoing trend in land drainage and watercourse channelization. In many watersheds, development has been so extensive that severely impacted aquatic resources provide little or no potential for fisheries or recreational use. Unfortunately, stream modification activities are generally immediate and permanent, resulting in total destruction of structure and function of entire natural wetland and riparian ecosystems. The impacts of stream modification have been the subject of numerous studies and are summarized in an excellent review by Simpson et al. (1982).

Figures on stream modification in the Rocky Mountains are difficult to obtain in the absence of formal ecoregion-wide studies. It is not clear in much of the information that is available whether reported estimates of habitat destruction refer to the stream channel, stream channel and riparian zone, or stream channel, riparian zone, and associated wetlands. For example, it has been estimated that as much as 70% of the overall riparian habitat associated with streams in the continental United States has been lost or altered. In some States and on certain watersheds, it has been estimated that as much as 95% of the habitat has been altered, with much of the loss associated with channelization activities. Between 1940 and 1971, the U.S. Army Corps of Engineers assisted in 889 stream development projects involving a total of 17,823 km (11,077 mi) of streams (Simpson et al. 1982). The Soil Conservation Service, as of 1979, was involved in channelization of 34,434 km (21,401 mi) of streams, and reported completion of 316,867 km (196,934 mi) of field drainage ditches, 625,595 km (388,810 mi) of drainage main or laterals, and 27,306 km (16,971 mi) of open channels "on the land" in 1976. Curiously, the SCS reported its efforts at stream improvements for fish in feet, at 3,839,152 (about 1,170 km or 727 miles). Accordingly, in 1971 Minnesota had 34,915 km (21,700 mi) of channelized stream, whereas the Minnesota Department of Natural Resources (1980) indicated that the total stream mileage in the State totaled 40,225 km (25,000 mi); an example of how reported data may be suspect of inaccuracies and innuendo.

Nowhere has the impact from a channelization project been better documented than in the Rocky Mountains of Montana (Baldes 1967, 1979). The study serves to illustrate the severity of within stream, upstream, and downstream negative impacts to the stream, riparian, and wetland habitats. Short-term and long-term impacts to the ecosystem were caused when a private landowner modified (channelized) 1,281 m (4,200 ft) of meandering Big Spring Creek into a 671 m (2,200 ft) straight ditch (Figure 97). About 0.4 ha (1 ac) of land usable to the landowner was initially gained at the time of the alteration. Destruction of property and habitat upstream and downstream from the channelization has been more severe than anyone anticipated.

Figure 97. Channelization of Big Spring Creek where a 1,281 m (4,200 ft) stream reach was changed to a 610 m (2,000 ft) ditch. (From Baldes 1967, 1979.)

Until the stream channel was straightened, the channel was normally full of water, provided good trout fishing, and the area was used for an annual fish derby. At that time, the banks were stable with very little erosion or change in channel configuration from year to year, regardless of low or high flows.

A 1938 aerial photo illustrated the site of the project location (Figure 98). The arrows point to the first bend upstream from the straightened area. In 1938, the channel upstream of the straightened area was 7.6 m (25 ft) wide; by 1953, it was 8.5 m (28 ft) wide, an erosion rate of .9 m (3 ft) in 15 years. In 1961, the area immediately downstream was channelized and straightened. In 1962, 1 year after being straightened, the channel was 13.1 m (43 ft) wide. By 1971, it was 50.3 m (165 ft) wide and, finally, by 1975, 145 m (476 ft) wide. From 1961 to 1971, a 10-year period, 37.2 m (122 ft) of stream bank eroded away as compared to 0.4 m (3 ft) in a 15-year period from 1938 to 1953. In 1975, major flooding accelerated the erosion rate and an additional 94.8 m (311 ft) of bank was lost. During one day the stream eroded nearly 30.5 m (100 ft) of bank.

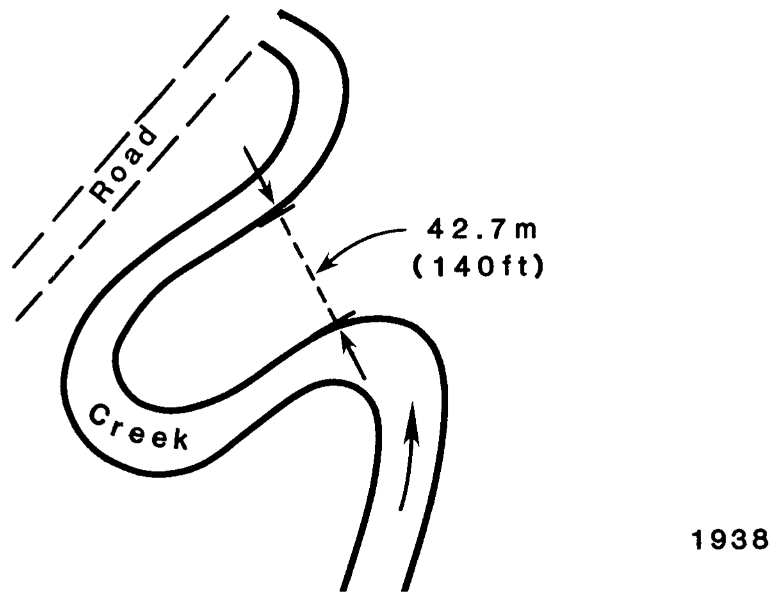

Figure 98. A sketch of a 1938 aerial photo illustrates channel configuration of a section of Big Spring Creek immediately upstream from the area to be channelized. (From Baldes 1967, 1979.)

To further illustrate the greatly accelerated erosion rate upstream from the straightened channel area, one must look at the distance across the point of land between the arrows. In 1938, the distance across the land was 42.7 m (140 ft). By 1953, the distance was 41.1 m (135 ft); very little erosion in a 15-year period. By 1961, the area downstream was straightened and in 1962 the distance between the arrows was 35.1 m (115 ft). By 1967, it was 12.8 m (42 ft) and, by 1971, only 2.9 m (9.5 ft) wide (Figure 99). Finally, in 1975, the meander was lost and the next upstream meander loop was also washed away.

When the 2.9 m (9.5 ft) meander and the next upstream meander washed away, something additional happened (Figure 100). A cross-section of the meander illustrates the water flow (towards you on the right side of the picture) around the peninsula-shaped piece of land (away from you on the left side of the picture). Note that the bottom of the channel is 1.0 m (3.4 ft) higher on the upstream side. When this 2.9 m (9.5 ft) of land washed away, the gradient (which is the elevation a stream channel drops per unit of length) increased 1 m (3.4 ft) in a 2.9 m (9.5 ft) distance. This drop plus a similar amount of drop that resulted when the next meander upstream also washed away, amounted to an additional 2.1 m (7 ft) of fall over a very short distance. Straightening the stream channel, always increases the gradient and water velocity. As a result of increased water velocity, accelerated erosion will occur immediately upstream as the stream attempts to re-establish its meander by vertical cutting within the channel (Tables 42 and 43).

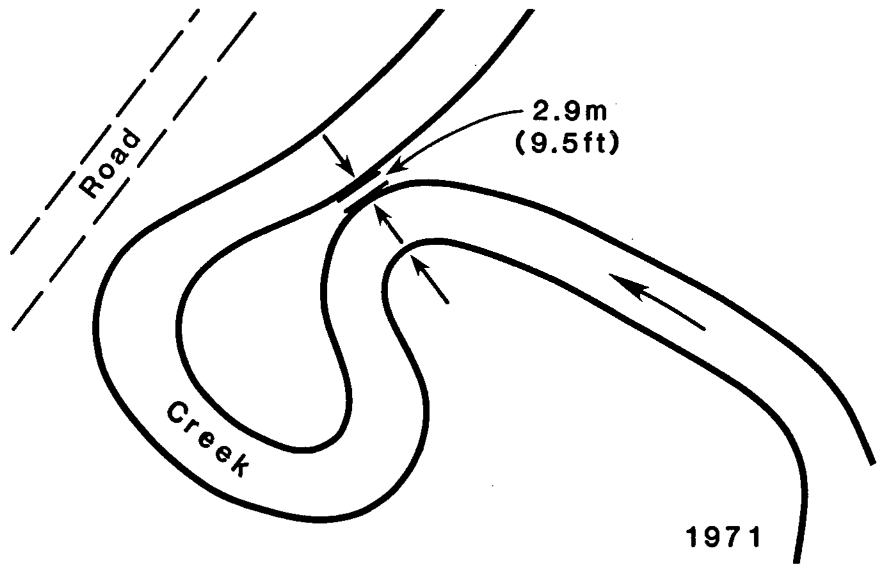

Figure 99. A sketch of a 1971 aerial photo illustrates channel configuration of the same portion of Big Spring Creek as Figure 98, 10 years following channelization. (From Baldes 1967, 1979.)

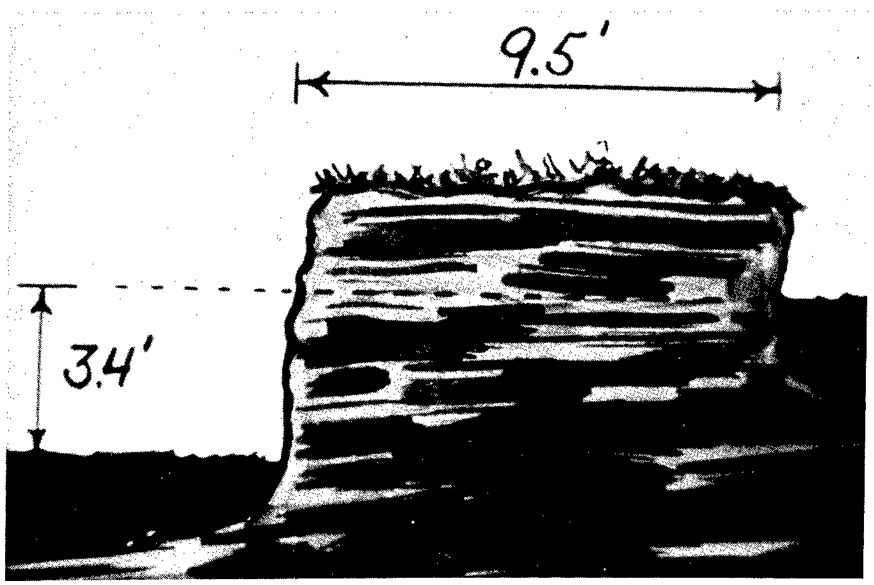

Figure 100. A cross section of the width of the peninsula and the decrease in channel gradient in the first upstream bend above the channelization. (From Baldes 1967, 1979.)

Table 42. Summary of channel changes in the first upstream meander following the straightening and channelization of a 1,281 m (4,200 ft) reach of Big Spring Creek. (From Baldes 1979.)

Year	Channel width m (ft)	Erosion m (ft)
1938	7.6 (25)	----
1953	8.5 (28)	0.9 (3)
1961	Straightened	----
1962	13.1 (43)	4.6 (15)
1967	40.5 (133)	27.4 (90)
1971	50.3 (165)	9.8 (32)
1975	145.1 (476)	94.8 (311)

Table 43. Summary of peninsula width changes at the first upstream meander. (From Baldes 1979.)

Year	Peninsula width m (ft)	Erosion m (ft)
1938 1953	42.7 (140) 41.2 (135)	1.5 (5) feet in 15 years
1961	Straightened	
1962 1971	35.1 (115) 2.9 (9.5)	32.0 (105) feet in 9 years

The Big Spring Creek erosion resulting from the channel modification was accelerated by flooding in 1975, but would have occurred in time even without major floods. This same erosion process takes place anytime a stream is straightened, regardless of the stream size or length of channel altered. Straightening a stream reach alters the gradient and meander patterns and accelerates the natural meander processes that usually occur over long periods of time.

Because of the increased gradient, caused by straightening, water flows through the upstream unmodified area faster (by guzzling or sucking action), cutting the channel deeper, and allowing the stream to erode against the more erodable gravel layer rather than the topsoil with its protective vegetative root system. The vertical cutting results in bank undercutting and a slumping of the streambank even during low stream flows. This head-cutting will continue until the stream again establishes a stable gradient.

Figures 101, 102, 103, and 104 illustrate the before, during, and after pictures of the erosion that occurred in 1975. The vertical cutting within the stream channel washed under the footings of the main highway bridge north of Lewistown. The bridge supports began to settle and cracks occurred.

As previously mentioned, an estimated 0.4 ha (1 ac) of land was gained as a result of the channel change but the adjacent upstream landowner lost about 3.2 ha (8 ac) of rich bottom land. The Soil Conservation Service estimated that 20,000 cubic yards of material was washed away in one year after the two meander loops described earlier cut through.

The 15,300 cu m (20,000 cu yds) of eroded material (bedload) ended up downstream. Part of the material was deposited as gravel across productive hay fields during the high water flow. The meander pattern downstream slowed water velocity and thereby permitted the heavier particles to settle out. Deposition of the bedload also occurred within the original channel, completely plugging it. This forced the water to cut several new channels through adjacent hay fields, again removing productive land and adding more tons of deposition to the downstream system, and in the process forming a braided channel. The massive bedload in the stream continues to cause problems as stream flows slowly shift it downstream.

The main road into a ranch, located 2.4 km (1.5 mi) below the channel change, washed out because the channel under the bridge became plugged with gravel. The stream was, once again, forced to cut several new channels through productive farm land.

Figure 101. Eroded streambank just prior to spring high water flow in 1975. (From Baldes 1979.)

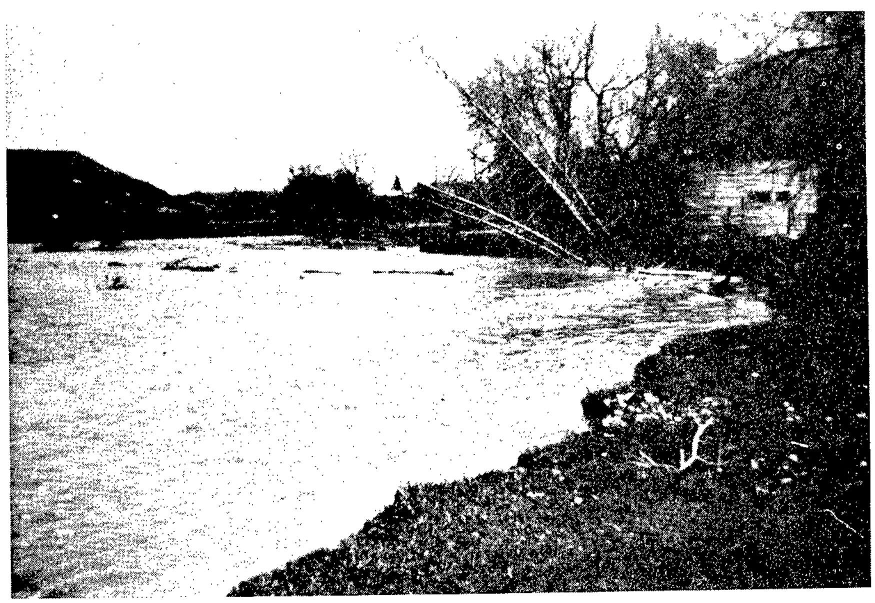

Figure 102. Erosion of streambank during high water in 1975. (From Baldes 1979.)

Figure 103. Extent of erosion following high water flow in 1975. (From Baldes 1979.)

Figure 104. Extent of erosion following high water flow in 1975. (From Baldes 1979.)

Finally, in 1978, the headcutting had progressed upstream over 610 m (2,000 ft), to where it threatened to undermine a large irrigation diversion structure, another bridge, and the center of Lewistown. A series of large, rock grade-stablization structures were installed in the channel, along with dikes, riprap, bank shaping, and fencing. This work cost the taxpayers approximately $260,000. A new highway bridge had to be constructed at a cost to the taxpayers of $199,000. Downstream bedload deposition areas required dredging from portions of the channel. Following dredging, banks were shaped, riprapped, and diked. Stream banks were fenced to exclude livestock so vegetative cover could again become established. This work cost the taxpayers $160,000, needs periodic maintenance, and there is no guarantee that it will last.

In spite of the expenditure of taxpayers' money approaching $750,000, the stream in many areas, particularly downstream, is very unstable and continues to erode and cause problems. Added to this should be the loss of productive agricultural land, destruction of fish and wildlife habitat, and inconvenience and cost to individual landowners along the stream.

Burning

Fires caused naturally by lightening, unintentionally by careless campers, and intentionally by land owners are frequent in the Rocky Mountains (Despain 1973). Burning wetlands affects nutrient transformation, increasing nutrient losses from organic combustion and flushing of dissolved minerals (Adamus and Stockwell 1983). When nutrients are not flushed out after burning, primary production may be greater on burnt sites from increased nutrient availability (Forrest and Smith 1975). Vegetation loss also affects nesting sites for birds (Gorenzel et al. 1981). Watershed deforestation from burning may take over 100 years to regain original characteristics (Stahelin 1943). Fires can also help create wetlands by impeding streams with fallen decaying trees (Stahelin 1943).

Clear-Cutting

Clearing vegetation for roads, brush control, or timber harvesting affects downslope wetland in a number of ways. Snowmelt is faster and earlier, and water retention is poorer in cleared areas (Leaf 1975a; DeBano et al. 1984). Greater water yield can also increase nutrient loading downstream, particularly of phosphorus, nitrogen, potassium, and suspended solids (Likens and Bormann 1974). Johnston (1984), however, found very little change in water chemistry, stream flow timing, annual water yield, and peak flow when 13% of an 88 ha (217 ac) aspen watershed was cleared in Utah. If road cuts are done carefully, watershed erosion can be minimized. Salting mountain roads during the winter, however, can increase runoff salinity, reducing numbers and diversity of stream invertebrates (Molles 1980), and possibly affecting plant species composition as well. One apparent benefit of clear-cutting, unrelated to wetlands, was reported by Crouch (1983). Removal of aspen overstory near Dolores, Colorado, had minimal adverse impact on nesting birds and actually improved their foraging sites.

Mining

The amount of environmental disturbance caused by the variety of mining operations in the Rocky Mountains is principally a function of the size of the operation. The significance of the environmental disturbance is a function of the type of substance mined, type and amount of waste produced, sensitivity of the operator to environmental problems, the nature of the surrounding environment (particularly the relationship to the surface waters of streams, lakes, ponds, wetlands, and ground water), and, in more recent years, regulatory requirements. The major ways that mining activities impact terrestrial, aquatic, and wetland ecosystems include: (1) production of toxic acid or alkaline mine drainages, waste disposal sites, and tailing area; (2) erosion and sedimentation; and (3) accidents.

It has been estimated that there are approximately 4,000 abandoned mines in Colorado. Although all of these do not constitute a point source of pollution, some do emit acid and alkaline waters into riverine wetland ecosystems, which degrades water quality and results in the destruction of fish and wildlife habitat in vast reaches. Estimates of the total miles of habitat pollution by mine drainage in Colorado range from 2,639 km (1,640 mi), by the Division of Wildlife (1970), to 720 m (450 mi), by the U.S. Geological Survey (1974). In either case, it becomes obvious that pollution is defined differently by different agencies and the actual number impacted may be somewhere in between.

These estimates do not take into consideration the probabilities of accidents by ongoing operations, such as pipeline leaks, equipment malfunction, settling pond failure, ore trucks skidding off roads, drilling mud that spills into wetlands and streams, unexpected water flows or runoff, and the wash-out of tailing dams.

Sand and Gravel Mining

The U.S. Fish and Wildlife Service identified 810,000 ha (2,000,000 ac) of fish and wildlife habitat damaged by surface mining in 1967 (U.S. Department of the Interior 1967). Much of the damage and destruction in the Rocky Mountains occurs in the narrow riparian wetland valley corridors. Conservative estimates place that figure at 972,000 ha (2,400,000 ac) in 1974. In 1964, producers reported to the U.S. Department of the Interior that 40% of the land disturbed by surface mining was by sand and gravel operations, and that sand and gravel was the largest nonfuel mining operation in the United States. The magnitude of these statistics became apparent with published estimates that production of sand and gravel was to double by 1980 and increase 300% to 400% by the year 2000.

Road and Railroad Access

Upon close inspection of appropriate mapping, it becomes clear that highway access to the many Rocky Mountain developments, villages, towns, and cities is by modern highways and railroads that have been constructed adjacent to medium-sized (stream orders 4, 5, 6) and large-sized (stream orders 7 to 12) riverine and riparian wetland ecosystems. Little highway or railroad

mileage is located along small (stream orders 1, 2, 3) systems. This concentration of roads along the limited number of medium and large streams has had critical and irreversible impact. Riparian wetland and riverine habitats have been destroyed and significantly reduced in size, have had vegetative structure and microclimate altered, wildlife disturbed, and wildlife habitat decreased. The negative impacts to water quality are on-going. Nevertheless, roads continue to be built, repaired, and enlarged to carry ever-growing numbers of vehicles with little overall regard for wetland losses or the long-term impact of such losses (Figure 105).

Grazing

Cattle and sheep grazing significantly impacts intermountain basin, subalpine, and montane wetland areas and mountain meadows throughout the Rocky Mountain west (Figure 106). Major effects include vegetation damage, reduction, and removal; soil compaction and erosion; and potable water degradation from fecal contamination (Menke 1977; Johnston and Brown 1979). Selective vegetation removal accelerates peatland erosion, reducing soil water, nutrient, and heavy metal retention capabilities. Since cattle prefer grasses, sedges, and willows, and sheep graze on forbs and willows, species shifts often occur in disturbed wet meadow plant communities (Ellison 1954). Grazing along riparian wetlands can also result in adverse effects, e.g., destruction of riverbanks (Platts 1981; Johnson and Carothers 1982).

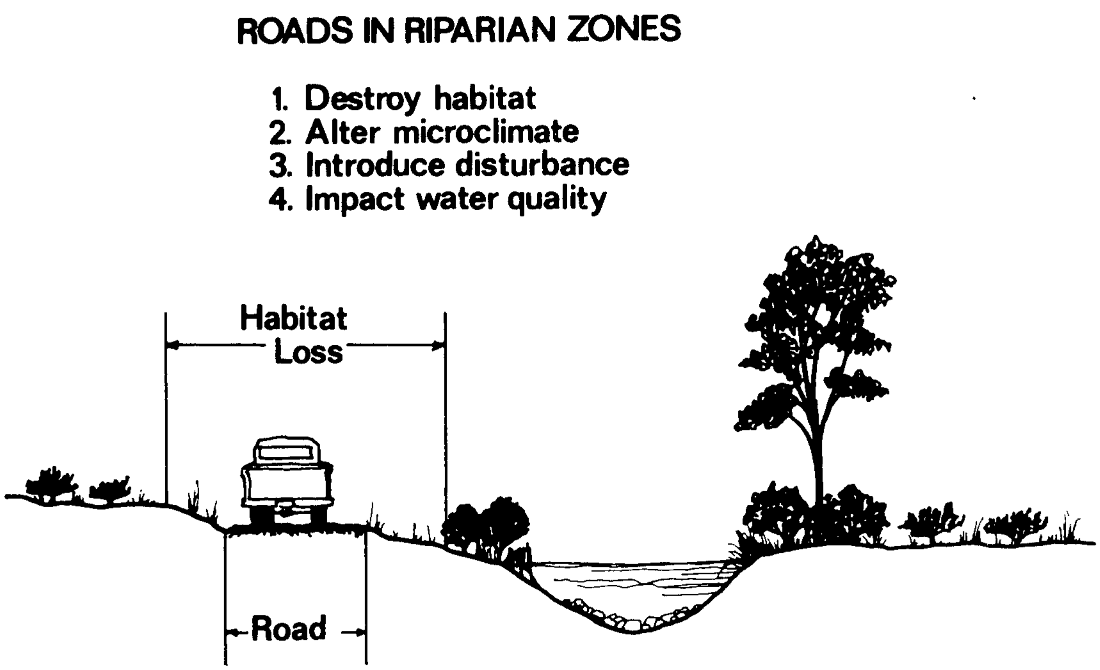

Figure 105. Road construction in riparian zones reduces their usefulness as wildlife habitat. Roads in riparian zones: (1) alter vegetative structure, (2) alter microclimate, (3) reduce the size of riparian zones, (4) disturb the wildlife, (5) impact water quality in the aquatic zone, and (6) destroy the wildlife habitat. (From Thomas et al. 1979.)

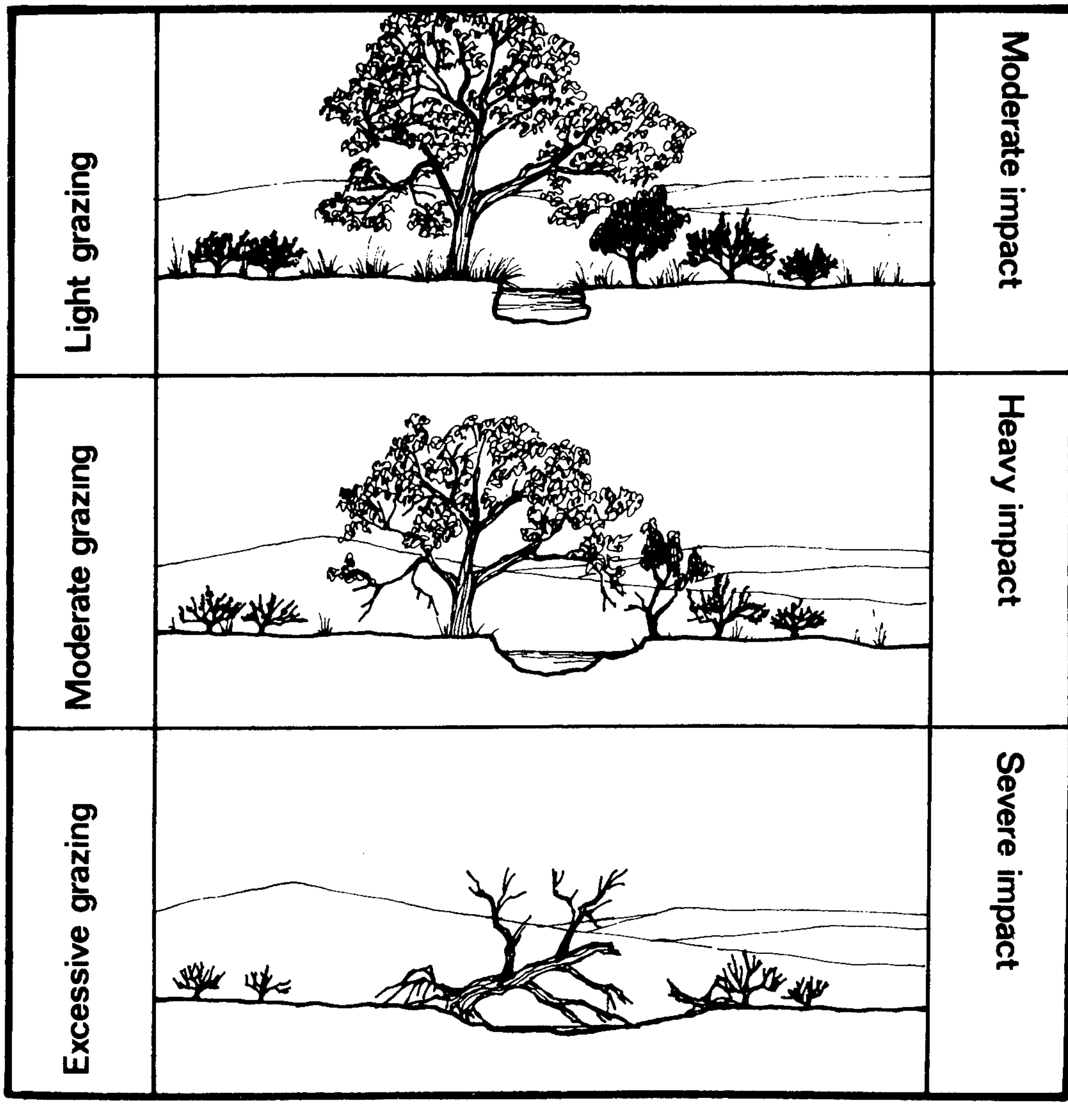

Figure 106. When livestock are grazed in riparian zones, consideraton of environmental impact is even more important than usual. (From Thomas et al. 1979.)

Cattle grazing is common in Rocky Mountain grassland parks and intermountain basins, willow stands often being primary foraging sites (Phillips 1977; Cannon and Knopf 1984). The Colorado Front Range supported 122,000 head of cattle in 1978, down from 300,000 head in 1950 (Johnson et al. 1978). The same authors contend that grazing rates of 1.2 ha per cow and calf caused no long-term impairment of water quality. Bacterial contamination from fecal streptococci and fecal coliforms represents the major water quality impact.

Leaf (1975b) concluded from an investigation in the central Rockies that cattle grazing destroyed plant cover, increasing soil erosion from exposed areas. There was little effect on surface runoff, however, since most stream flow and sediment yield occur during spring snowmelt, prior to summer grazing.

Dams and Reservoirs

The U.S. Fish and Wildlife Service National Reservoir Research Program (NRRP) conducted four National inventories of reservoirs since 1960 (Ploskey and Jenkins 1980). Reported data represent information provided by State fishery agencies and include a compilation of reservoirs, arrayed by State, listed by name, and average annual surface area. The goal of the inventories was to identify those man-made impoundments where the aquatic environment has been markedly influenced by reservoir design or operation.

For purposes of the inventories, a "reservoir" is defined as an impoundment with a mean annual pool of 202 ha (500 ac) or more. Where a dam regulates a natural lake, the resulting impoundment is not considered a "reservoir" unless the original area or volume is more than doubled. Surface area is expressed in acres at average annual pool, when data are available. If unavailable, either normal conservation, summer, operating, or power pool area is listed.

Over 1,600 reservoirs larger than 202 ha (500 ac) presently exist in the United States, which, at average water levels, collectively comprise approximately 4.1 million ha or 10 million surface acres. A separate inventory conducted under the 1972 National Dam Inspection Act revealed about 49,000 non-Federal dams, most of which are privately owned. Therefore, in addition to the over 1,600 large Federal dams, the 49,000 non-Federal dams puts the U.S. total over 50,600. The grand total surface area remains unknown, but is much in excess of 10 million surface acres.

Although information is lacking, the 1980 NRRP inventory indicated a total of 171 major reservoirs in the six Rocky Mountain States covered in this profile. The number of smaller privately-owned reservoirs has not been recently determined, but has been estimated to be many times greater than the number of large Federal projects. In each case, reservoir projects encompass riverine, riparian, and wetland areas, and the total acreage continues to decrease with each finished project. Most projects are located on the medium- or large-sized stream reaches because small-sized stream reaches (i.e., first, second, and third order stream reaches) do not produce enough water to qualify as sites for major reservoir projects.

Acid Precipitation

Acid precipitation caused by industrial emission (Likens et al. 1972) may affect Rocky Mountain region wetlands, but data are lacking (Oppenheimer et al. 1985). Bulk, atmospheric deposition from 42 sites in Colorado demonstrated increased precipitation acidity with elevation (Lewis and Grant 1984). High levels of NO_2 and SO_2 from power plant emissions were responsible for lowering pH. At lower elevations, the acidity was partially neutralized by carbonates from alkalis swept up into the atmosphere, hence the inverse relationship between precipitation, pH, and elevation. Stream water analyses in Como

Creek, Colorado, elevation 2,900 m (9,515 ft), showed decreases in bicarbonate and total cations, and increases in sulfate, nitrate, ammonia, and dissolved organic matter output with increased precipitation acidity (Lewis and Grant 1979b). Since wetlands have acid soils, the changes by added acid precipitation will be slight until the increase in acid precipitation is great.

6.5 ENVIRONMENTAL PROTECTION OF ROCKY MOUNTAIN WETLANDS

Environmental legislation and statutes, as currently implemented in the United States, are heavily predicated on concern about man-caused (anthropogenic) impacts on palustrine and riverine wetland ecosystems. Federal legislation mandated by the Fish and Wildlife Coordination Act (1958), National Environmental Policy Act (1969), Coastal Zone Management Act (1976), Clean Water Act (1972), and other State and Federal statutes, clearly provides mechanisms for protecting the integrity of our inland water, wetland, and marine environments, while utilizing them for beneficial uses.

Section 10 of the Rivers and Harbors Act and Sections 401 and 404 of the Clean Water Act (1972) provide for Federal regulation of small habitat modifications and continue to be the subject of heated debate and outright hatred of Federal intervention on private property rights. In addition to the Federal legislation, a number of Federal Presidential Executive Orders, such as Protection of Wetlands (Executive Order 11990) and Flood Plain Management (Executive Order 11988), are specifically concerned with controlling the cumulation of habitat modifications to riverine and palustrine wetland habitats from "piecemeal" development impacts.

6.6 NATIONAL WETLANDS POLICY

Under Section 404 of the Clean Water Act of 1972 (P.L. 92-500), Congress extended regulatory jurisdiction of the U.S. Army Corps of Engineers beyond the traditional "navigable waters," as defined by the 1899 Rivers and Harbors Act, to cover "all waters of the United States"--including wetlands. EPA was made a partner in the act, with veto authority and responsibility for establishing guidelines for protection of the aquatic environment. Although it is rarely mentioned, Section 404(s)(4) provides for stiff civil and criminal penalties for willful or negligent violation of any condition contained in a 404 permit, including fines as high as $50,000 per day and imprisonment of up to two years.

Whereas Section 404 does not cover the variety of activities regulated by the 1899 Rivers and Harbors Act, it does require permits for all construction on public and private lands involving the discharge of dredged or fill materials into the waters of the United States, including wetlands. All permit applications now processed involve assessment of each project's environmental impacts; however, normal agricultural, forestry, and ranching operations do not require permits.

Section 404 of the Clean Water Act (1972 and 1977) and the associated permitting process for impacting the waters and wetlands of the United States created a critical need to be able to precisely identify, classify, functionally evaluate, and quantify potential impacted acreages of wetlands. Every 404 permit application (see later) must undergo an extensive "public interest review" to balance the foreseeable project benefits and detriments. Factors that must be considered include: conservation, economics, esthetics, environment, historical values, fish and wildlife values, flood damage prevention, land use, recreation, water quality, water supply, and others. The act states that "no permit will be granted unless its issuance is found to be in the public interest." It must be determined that the "benefits of the proposed alteration (to wetlands) outweigh the damage to the wetland resource and the proposed alteration is necessary to realize those benefits." Although a particular alteration of wetlands may constitute a minor change, the cumulative effect of numerous such piecemeal changes often results in a major impairment of the wetland resources. Thus, the particular wetland site for which an application is made requires evaluation with the recognition that it is part of a complete and interrelated wetland ecosystem.

Dredging refers to digging to produce a spoil (i.e., the material dug). The deposition of dredged spoil is a major problem and the sheer volume of spoil produced can create serious pollution and land-use problems. Sediments removed from streams, estuaries, and harbor bottoms, particularly in industrialized urban areas, frequently contain toxic heavy metals and organic chemicals. When redeposited in waters or on wetlands, these toxic substances have the potential to enter food chains and water supplies, smother bottom and wetland habitat, and increase water turbidity.

Fill is virtually any solid material, permanently placed in the water or wetland, that replaces an aquatic area with dry land or changes its bottom elevation. Fill, likewise, can increase turbidity and pollute water with toxic substances. Of prime concern with fill is that man-caused activities can make major alterations in aquatic ecosystems and change the hydrological character of watercourses.

Considerable strength for protection of wetlands was given upon issuance of Executive Order 11990 by the President of the United States in 1977. The order was prepared to avoid, to the extent possible, the long- and short-term adverse impacts associated with the destruction or modification of wetlands and to avoid direct or indirect support of new construction in wetlands wherever there is a practicable alternative. By virtue of the National Environmental Policy Act of 1969 (NEPA) and Executive Order (EO) 11990, Federal agencies were mandated to consider a number of factors relevant to a proposal to modify a wetland on public or private lands, including:

> public health, safety, and welfare, including water supply, quality, recharge and discharge; pollution; flood and storm hazards; and sediment and erosion;
>
> maintenance of natural systems, including conservation and long-term productivity of existing flora and fauna, species and habitat diversity and stability, hydrologic utility, fish, wildlife, timber, and food and fiber resources; and

other uses of wetlands in the public interest, including recreational, scientific, and cultural uses.

The term "new construction" includes draining, dredging, channelizing, filling, diking, impounding, and related activities and any structures or facilities begun or authorized after the effective date of the order.

A second Executive Order (11988), on Flood Plain Management, was issued on the same date in 1977 as EO 11990. It directs each Federal agency to take necessary action to reduce the risk of flood loss and to restore and preserve the natural and beneficial values served by floodplains whenever it undertakes a Federally "assisted" construction or improvement. The order specifically includes Federal regulatory and permitting activities and directs each Federal agency to:

take floodplain management into account when formulating or evaluating any water or land use plan; and

require land and water resources use appropriate to the degree of hazard involved.

Under the order, the term "floodplain" applies to lowland and flat areas adjoining inland waters (streams) and includes the area subject to a 1% or greater chance of flooding in any given year. The order has been interpreted as directing each agency to take affirmative action to reduce flood risk and to restore and preserve natural resources afforded by floodplains, not merely to consider floodplain protection in decisionmaking.

Public interest in wetlands and wildlife has escalated along with the ever-increasing human population, environmental awareness, and increased leisure time. Sportsmen are no longer the only interest group, because wetlands have appeal by serving as outdoor laboratories for education classes from elementary through advanced college levels. Wetlands are frequented by birdwatchers, hikers, canoeists, nature photographers, and others interested in seeing as many different kinds of wildlife and as many of each kind as possible.

Public awareness of the values of wetlands as nutrient, sediment, and pollution traps also has risen, and the public is continuing to demand high-quality performance of public agencies and the private sector.

CHAPTER 7

SUMMARY AND CONCLUSIONS[1]

7.1 SUMMARY

A thorough search of literature on wetlands of the Rocky Mountains has been accomplished. This search indicates that most investigations to date have been on vegetational characteristics of various types of wetlands. Little has been done on processes and functions of wetlands in the Rocky Mountains, outside of description of classic successional processes. No research has been reported on values of Rocky Mountain wetlands, but some recent work has been accomplished on effects of impacts.

Any discussion of Rocky Mountain wetlands is dependent on a thorough understanding of the geology, hydrology, and climate of the region. While geology and climate have been studied extensively, and the hydrology of the Rocky Mountains is generally understood, little hydrologic research has been conducted specifically on wetlands. Variations within this vast area make generalization very difficult. However, our knowledge base is adequate for making management decisions about the general consequences of developmental activities on Rocky Mountain wetlands.

We do know from the published literature that there is a wide variety of wetland types, despite the small proportion of the land area of the Rocky Mountains that is in wetlands. About 80 community types are described for the Rocky Mountains in the published literature. These community types have been organized and described based on an international classification scheme and integrated into the Cowardin (1979) system of the U.S. Fish and Wildlife Service. This system accurately reflects the ecological relations among wetland communities in the field.

The extensive field work done in conjunction with developing information for the 404 permitting process indicates that management of wetlands in the Rocky Mountains needs to begin with a knowledge of the types and amounts of remaining wetlands. Also, much is known about the influences of human activity on Rocky Mountain wetlands that have occurred over a 120-year period. It is clear that the original amount of wetland area in the Rocky Mountains has been decreased by about one-third since the "opening of the West."

[1]Authored by B. E. Willard.

There is a wide range of intrinsic and extrinsic values of Rocky Mountain wetlands, as discussed in this report. The literature review shows, however, that there have not been many specific or in-depth investigations of values of Rocky Mountain wetlands. Therefore, deduction of Rocky Mountain wetland values is based on knowledge of wetland values from other regions.

7.2 CONCLUSIONS

At this juncture in our knowledge of wetlands in the Rocky Mountains, we can conclude that, although the areal extent of wetlands is small by comparison to some other regions of the Nation, there is a wide variety of wetland types, ranging from the intermountain basins to the alpine tundra. Much is known about human impacts on these various wetlands, especially those in the montane region and the intermountain basins. Very little is known about the ecological processes and functions of Rocky Mountain wetlands or about their intrinsic values.

Knowledge of the structure, functions, and values of wetlands is the most important factor in decisionmaking about their use. Therefore, considerable investment of scientific resources and monies is needed in a wide range of research areas to bring the knowledge of these valuable communities up to current demands. Appendix D contains a listing of specific research needs that we believe should be considered for major funding to further knowledge of Rocky Mountain wetlands. Much more specific information about Rocky Mountain wetlands must be gathered, before any one of the types can be analyzed in an ecosystem manner. But this is a research need that should be anticipated as the background investigations proceed. Such an effort will have at least four major benefits: (1) it will provide a clearer picture of the interrelationships among the various factors operating in any single wetland; (2) it will enable researchers to determine the interrelationships between different types of adjacent wetlands; (3) these two knowledge bases will enable decisionmakers and policymakers to operate from a more accurate viewpoint; and (4) resultant information will offer users a much more accurate assessment of the values and benefits that they derive from wetlands without direct involvement in their operation.

The benefits of systems-type research on Rocky Mountain wetlands are sufficiently large and far-reaching that thought should begin immediately about how to finance such a long-term, large-scale research program.

LITERATURE CITED

Adamus, P. R. 1983. A method for wetland functional assessment: Volume II. FHWA assessment. FHWA-IP-82-24. Washington, DC. 138 pp.

Adamus, P. R., and L. T. Stockwell. 1983. A method for wetland functional assessment: Volume I. Critical review and evaluation concepts. FWHA-IP-82-23. Washington, DC. 181 pp.

Allan, J. S. 1962. The plant communities of the Big Cottonwood Canyon drainage. M.S. Thesis. University of Utah, Salt Lake City. 108 pp.

Allen, H. L. 1980. Floodplain plant communities of the North Fork, Flathead River, Montana. National Park Service, Glacier National Park. 98 pp.

Almand, J. D., and W. B. Krohn. 1978. The position of the Bureau of Land Management on the protection and management of riparian ecosystems. Pages 359-361 _in_ R. R. Johnson and J. F. McCormick, tech. coords. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-12. Washington, DC.

American Fisheries Society, Western Division. 1980. Position paper on management and protection of western riparian stream ecosystems. American Fisheries Society, Bethesda, MD. 24 pp.

Anderson, D. R. 1967. Effects of water manipulation on waterfowl production and habitat. M.S. Thesis. Colorado State University, Ft. Collins. 60 pp.

Anderson, M. G., and J. P. Low. 1976. Use of sago pondweed by waterfowl on the Delta Marsh, Manitoba. J. Wild. Mgmt. 40:233-242.

Anderson, S. H. 1982. Effects of the 1976 Seney National Wildlife Refuge wildfire on wildlife and wildlife habitat. U.S. Department of the Interior. FWS Resource Publication 146. 28 pp.

Arner, D. H. 1963. Production of duck food in beaver ponds. J. Wildl. Mgmt. 27:76-81.

Attfield, R. 1983. The ethics of environmental concern. Columbia University Press, New York. 215 pp.

Atwood, W. W. 1945. The Rocky Mountains. Vanguard Press, NY. 324 pp.

Auclair, A. N. D., A. Bouchard, and J. Pajaczkowski. 1976. Productivity relations in a _Carex_-dominated ecosystem. Oecologia 26:9-31.

Bailey, R. G., and C. T. Cushwa. 1981. Ecoregions of North America, after the classification of D. M. Crawley. U.S. Fish Wildl. Serv. FWS/OBS-81/29. 1 map.

Baldes, R. 1967. Big Spring Creek. Presentation at the Annual Meeting of the Colorado/Wyoming Chapter of the American Fisheries Society.

________. 1979. Big Spring Creek. Presentation at the 15th Annual Meeting of the Colorado/Wyoming Chapter of the American Fisheries Society.

Baldwin, J. L. 1973. Climates of the United States. U.S. Dept. of Commerce, Washington, DC. 74 pp.

Bamberg, S., and J. Major. 1968. Ecology of the vegetation and soil associated with calcareous parent materials in three alpine regions of Montana. Ecol. Monogr. 38:127-167.

Barel, D., and R. J. Barsdate. 1978. Phosphorus dynamics of wet coastal tundra soils near Barrow, Alaska. Pages 516-537 in D. C. Adriano and I. L. Brisbin, eds. Environmental chemistry and cycling processes: Proceedings of symposium, Augusta, GA, 28 April - 1 May 1976. Washington: U.S. Department of Energy Symposium Series CONF-760429.

Barry, R. G. 1973. A climatological transect on the east slope of the Front Range, Colorado. Arct.-Alp. Res. 5:89-110.

__________. 1981. Mountain weather and climate. Methuen and Co., London. 313 pp.

Batie, S. S., and J. R. Wilson. 1978. Economic values attributable to Virginia's coastal wetlands as inputs in oyster production. Southern J. of Agric. Econ. 29:110-118.

Batzli, G. O. 1981. Populations and energetics of small mammals in the tundra ecosystem.

Bay, R. R. 1969. Runoff from small peatland watersheds. J. Hydrol. 9:90-102.

Bazsilier, K., U. Grauhall, and T. A. Stenstrom. 1978. Nitrogen fixation in wet minerotrophic moss communities of a subarctic mine. Oikos 31:236-246.

Beadle, N. C. W., and A. B. Costin. 1952. Ecological classification and nomenclature. Proc. Linnean Soc. of New South Wales, LXXVII 61-82.

Behnke, R. J. 1968. Rare and endangered species: the native trouts of Western North America. Proc. West. Assoc. State Game Fish Comm. 48:533-535.

Behnke, R. J., and M. Zarn. 1976. Biology and management of threatened and endangered Western trouts. USDA, For. Serv. Gen. Tech. Rept. RM-28. 45 pp.

Beidleman, R. G. 1978. The cottonwood willow riparian ecosystem as a vertebrate habitat, with particular reference to birds. Pages 192-195 in W. D. Graul and S. J. Bissell, eds. Lowland river and stream habitat in Colorado: A symposium. Colorado Chap. Wildl. Soc. and Colorado Audubon Council.

Benedict, J. B. 1970. Downslope soil movement in a Colorado alpine region: rates, processes, and climatic significance. Arct. Alp. Res. 2:165-226.

Benson, P. C. 1979. Land use and wildlife with emphasis on raptors. USDA Forest Serv. Intermt. Reg. 32 pp.

Bernard, J. M. 1973. Production ecology of wetland sedges: the genus _Carex_. Pol. Arch. Hydrobiol. 20:207-214.

Bernard, J. M., and J. G. MacDonald, Jr. 1974. Primary production and life history of _Carex lacustris_. Can. J. Bot. 52:117-123.

Berry, J. W. 1968. Climate of Colorado. Page 74 _in_ Climatology of the United States. No. 60-S. U.S. Dept. of Commerce. NOAA, EDS, Washington, DC.

Bierly, K. F. 1972. Meadow and fen vegetation in Big Meadows, Rocky Mountain National Park. M.S. Thesis. Colorado State University, Fort Collins. 102 pp.

Billings, W. D. 1969. Vegetational pattern near alpine timberline as affected by first snowdrift interaction. Vegetation 19:192-207.

Billings, W. D., and L. C. Bliss. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. Ecology 40:389-397.

Billings, W. D., and H. A. Mooney. 1959. An apparent frost hummock sorted polygon cycle in the alpine tundra of Wyoming. Ecology 40:16-20.

Black, C. A. 1968. Soil plant relationships. John Wiley, New York. 792 pp.

Bliss, L. C. 1966. Plant productivity in alpine microenvironments on Mt. Washington, New Hampshire. Ecol. Monogr. 36:125-155.

Boelter, D. H. 1970. Important physical properties of peat material. Pages 150-154 _in_ Proc. Third Intl. Peat Congr., 1968. Quebec.

Boldt, C. E., D. W. Uresk, and K. Severson. 1978. Riparian woodlands in jeopardy on northern high plains. Pages 184-189 _in_ R. R. Johnson and J. F. McCormick, tech. coords. Strategies for protection and management of flood-plain wetlands and other riparian ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-12. Washington, DC.

Bolen, E. G. 1964. Plant ecology of spring-fed salt marshes in western Utah. Ecol. Monogr. 34:143-166.

Bond, H. W. 1979. Nutrient concentration patterns in a stream draining a montane ecosystem in Utah. Ecology 60:1184-1196.

Bonham, C. D., and R. T. Ward. 1970. Phytosociological relationships in alpine tufted hairgrass (_Deschanpsia caespitosa_) meadows. Arct. Alp. Res. 2:267-275.

Boyce, D. 1977. Vegetation of the South Fork of the White River Valley, Colorado. Ph.D. Dissertation. University of Colorado, Boulder. 328 pp.

Boyd, C. E. 1970a. Losses of mineral nutrients during decomposition of _Typha latifolia_. Arch. Hydrobiol. 66:511-512.

__________. 1970b. Influence of organic matter on some characteristics of aquatic soils. Arch. Hydrobiologia 36:17-21.

__________. 1970c. Chemical analyses of some vascular aquatic plants. Arch. Hydrobiologia 67:78-85.

__________. 1970d. Amino acid, protein, and caloric content of vascular aquatic macrophytes. Ecology 51:902-906.

__________. 1978. Chemical composition of wetland plants. Pages 155-167 _in_ R. E. Good, D. F. Whigham, R. L. Simpson, eds. C. G. Jackson, tech. ed. Freshwater wetlands: ecological processes and management potential. Academic Press, New York, NY.

Braun, C. E. 1969. Population dynamics, habitat, and movements of white-tailed ptarmigan in Colorado. Ph.D. Dissertation. Colorado State University, Ft. Collins. 189 pp.

Braun, C. E., R. W. Hoffman, and G. E. Rogers. 1976. Wintering areas and winter ecology of white-tailed ptarmigan in Colorado. Colorado Div. Wildl. Spec. Rep. No. 38. 38 pp.

Bray, J. R. 1960. The chlorophyll content of some native and managed plant communities in Central Minnesota. Can. J. Bot. 38:313-333.

Bray, J. R., D. B. Lawrence, and L. C. Pearson. 1959. Primary production in some Minnesota terrestrial communities. Oikos 10:38-49.

Brayton, S. 1983. Eager beavers improve stream habitats in Wyoming. Wyoming Horizons 8:1.

Breckenridge, R. P., L. R. Wheeler, and J. F. Ginsburg. 1983. Biomass production and chemical cycling in a manmade geothermal wetland. J. Soc. Wetland Sci. 3:26-43.

Brown, S., M. M. Brinson, and A. E. Lugo. 1978. Structure and function of riparian wetlands. Pages 17-31 _in_ R. R. Johnson and J. F. McCormick, tech. coords. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-12. Washington, DC.

Brown, D. E., C. H. Lowe, and C. P. Pase. 1979. A digitized classification system for the biotic communities of North America, with community (series) and association examples for the Southwest. J. Arizona-Nevada Acad. Sci. 14:1-16.

Brown, T. C., and T. C. Daniel. 1984. Modeling forest scenic beauty: concepts and applications to ponderosa pine. USDA For. Serv. Gen. Tech. Res. Pap. RM-256. Fort Collins, CO. 35 pp.

Buckner, D. L. 1977. Ribbon forest development and maintenance in the central Rocky Mountains of Colorado. Ph.D. Thesis. University of Colorado, Boulder. 224 pp.

Bunin, J. E. 1975. The vegetation of the west slope of Park Range, CO. Ph.D. Dissertation. University of Colorado, Boulder. 235 pp.

Burt, W. H., and R. P. Grossenheider. 1952. A field guide to the mammals. Houghton Mifflin Co., Boston. 200 pp.

Butterfield, B., and R. G. Wright. 1983. Great blue heron nesting on the North Fork of the Flathead River, Montana. University of Idaho C.P.S.U. Rept. B83-4. 27 pp.

Caine, T. N. 1982. Water and sediment flows in the Green Lakes Valley, Colorado Front Range. Pages 13-22 in J. C. Halfpenny, ed. Ecological studies in the Colorado alpine. University of Colorado, Institute of Arctic and Alpine Research Occasional Paper No. 37, Boulder, CO.

Cannon, R. W., and F. L. Knopf. 1984. Species composition of a willow community relative to seasonal grazing history in Colorado. Southwest Nat. 29:234-237.

Carson, R. 1962. The silent spring. Houghton Mifflin, Burlington, MD. 368 pp.

Carter, V., M. S. Bedinger, R. P. Novitzki, and W. O. Wilen. 1979. Water resources and wetlands. Pages 344-379 in P. E. Greeson, J. R. Clark, and J. E. Clark, tech. coords. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Chadwick, D. H. 1985. Mt. Haven of the trumpeters. Defenders 60:20-30.

Chapin, F. S. III. 1981. Field measurement of growth and phosphate absorption in Carex aquatilus along a latitudinal gradient. Arct. Alp. Res. 13:83-94.

Chapin, F. S., R. J. Barsdate, and D. Barel. 1978. Phosphorus cycling in Alaskan coastal tundra: a hypothesis for the regulation of nutrient cycling. Oikos 31:189-199.

Chapin, F. S., and A. Bloom. 1976. Phosphate absorption: adaptation of tundra graminoids to a low temperature, low phosphorus environment. Oikos 27:111-121.

Chapman, D. M. 1974. An interpretive master plan for Arapahoe National Wildlife Refuge, Colorado. M.S. Thesis. Colorado State University, Ft. Collins. 69 pp.

Chase, W. D., III, S. J. Bissell, H. E. Kingery, and W. D. Wood. 1982. Colorado bird distribution latilong study. Colorado Field Ornithologists in cooperation with the Colorado Div. of Wildlife, Denver, CO. 78 pp.

Clark, J. 1979. Freshwater wetlands: habitats for aquatic invertebrates amphibians, reptiles, and fish. Pages 330-343 in P. E. Greeson, J. R. Clark and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Clark, T. W., and R. D. Dorn, eds. 1981. Rare and endangered vascular plants and vertebrates of Wyoming, 2nd ed. Box 2705, Jackson, WY 83001. 26 pp.

Clements, F. E. 1905. Research methods in ecology. University Publishing Co., Lincoln, NE. 334 pp.

______________. 1916. Plant succession. Carnegie Institute of Washington Publication 242. 512 pp.

Collins, E. I., R. W. Lichvar, and E. F. Evert. 1984. Description of the only known fen-palsa in the contiguous United States. Arct. Alp. Res. 16:155-158.

Colorado Division of Wildlife. 1970. Mimeograph report. Denver, CO. 14 pp.

Cook, S. E. 1976. Quest for an index of community structure sensitive to water pollution. Environ. Poll. 11:269-288.

Cooper, D. J. 1984. Vegetation of the mountain parks. Pages 5-12 in D. J. Cooper, ed. Ecological survey of the City of Boulder, Colorado, mountain parks. City of Boulder Parks and Recreation Dept., Boulder, CO.

______________. 1986. Wetlands of the Cross Creek Valley, Holy Cross Wilderness Area, Colorado. Holy Cross Wilderness Defense Fund Publication. Tech. Rept. 2. 24 pp.

Cooper, W. S. 1912. Ecological succession of mosses as illustrated upon Isle Royale, Lake Superior. Plant World 15:197-213.

______________. 1923. The recent ecological history of Glacier Bay, AK. Ecology 4:93-128, 223-246, 355-365.

Cope, O. B., ed. 1979. Grazing and riparian/stream ecosystems. Proc. of the Forum. Denver, CO., Nov. 3-4, 1978. Trout Unlimited, Inc., Denver, CO. 94 pp.

Cordell, G. V., Jr. 1971. Climate of Montana. In Climatography of the United States. No. 6024 USDC, NOAA, EDS. Washington, DC.

Council on Environmental Quality. 1978. Our Nation's wetlands. An interagency task force report. U.S. Govt. Printing Office. 70 pp.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish Wildl. Serv. FWS/OBS-77/31. 103 pp.

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gazette 27:95-117, 167-202, 281-308, 361-391.

Crisp, D. T. 1966. Input and output of minerals for an area of Pennine moorland: the importance of precipitation, drainage, peat erosion, and animals. J. Ecol. 54:327-348.

Crouch, G. L. 1983. Effects of commercial clear-cutting of aspen on understory vegetation and wildlife habitat values in southwestern Colorado. USDA For. Serv. Res. Pap. RM-246. Fort Collins, CO. 8 pp.

Crow, J. H., and K. B. MacDonald. 1979. Wetland values: Secondary production. Pages 146-161 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Cummins, K. W. 1973. Trophic relations of aquatic insects. Ann. Rev. Entomol. 18:183-206.

____________. 1974. Structure and function of stream ecosystems. Bioscience 24:631-641.

____________. 1975. The ecology of running water: theory and practice. Pages 277-293 in International joint symposium on the Great Lakes, Sandusky River Basin Symposium, May 2-3. Heidelburg College, Tifflin, OH.

____________. 1977. From headwater streams to rivers. Am. Biol. Teach. 1977:305-312.

Dansereau, P., and F. Segadas-Vianna. 1952. Ecological study of the peat bogs of eastern North America. I. Structure and evolution of vegetation. Can. J. Bot. 30:490-520.

Darnell, R. M. 1979. Impact of human modifications on the dynamics of wetland systems. Pages 200-209 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Daubenmire, R. F. 1941. Some ecologic features of the subterranean organs of alpine plants. Ecology 22:370-378.

____________. 1943. Vegetational zonation in the Rocky Mountains. Bot. Review 9:325-393.

____________. 1968. Plant communities: a textbook of plant synecology. Harper and Row, New York, Evanston, London. 300 pp.

____________. 1974. Plants and environment: a textbook of plant autecology, 3rd ed. J. Wiley and Sons, New York. 422 pp.

Davis, G. J., and M. M. Brinson. 1980. Responses of submersed vascular plant communities to environmental change. U.S. Fish Wildl. Serv. FWS/OBS-79/33. 69 pp.

Davis, R. J. 1952. Flora of Idaho. Wm. C. Brown Co., Dubuque, IA. 828 pp.

Day, F. P. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63:670-678.

DeBano, L. F., J. J. Brejda, and J. H. Brock. 1984. Enhancement of riparian vegetation following shrub control in Arizona chaparral. J. Soil and Water Conserv. 39(5):317-320.

de la Cruz, A. A. 1978. Primary production processes: summary and recommendations. Pages 79-86 in R. E. Good, ed. Freshwater wetlands: ecological processes and management potential. Academic Press, New York.

De Leuw, Cather and Company. 1977. Vegetation sampling (Glenwood Canyon). Unpubl. report prepared for Colo. Div. of Highways, Glenwood Springs, CO. De Leuw, Cather and Co., Chicago, IL.

Denniston, R. H., II. 1956. Ecology, behavior and population dynamics of the Wyoming, or Rocky Mountain, moose, Alcesi alces shirasi. Zoologica 41(14):105-118.

Despain, D. G. 1973. Vegetation of the Big Horn Mountains, Wyoming, in relation to substrate and climate. Ecol. Monogr. 43:329-355.

DeVelice, R., J. A. Ludwig, W. H. Moir, and F. Ronco, Jr. 1984. A classification of forest habitat types of northern New Mexico and southern Colorado. USDA For. Serv. Gen. Tech. Rept. RM. Ft. Collins, CO. 173 pp.

Dick-Peddie, W. A. 1985. New Mexico vegetation. [In preparation.]

Dingman, S. L. 1966. Characteristics of summer runoff from a small watershed in Central Alaska. Water Resources Res. 2:751-754.

Dix, R. L., and F. E. Smeins. 1967. The prairie, meadow, and marsh vegetation of Nelson County, North Dakota. Can. J. Bot. 45:21-58.

Dix, R. L. 1974. Regional ecological systems of Colorado. Pages 7-17 in P. O. Foss, ed. Environment and Colorado: a handbook. Env. Res. Center, Colorado State University, Fort Collins.

Dixon, H. 1935. Ecological studies on the high plateaus of Utah. Bot. Gazette. 97:272-320.

Dixon, H. N. 1971. Flora of the San Luis Valley. New Mexico Geol. Soc. Publ. #235, pp. 133-136.

Dodson Gray, E. 1981. Green paradise lost. Roundtable Press, Wellesley, MA. 166 pp.

Donnelly, D. M., C. F. Sorg, J. B. Loomis, and L. J. Nelson. 1985a. Net economic value of hunting and fishing in Idaho. Rocky Mt. For. and Range Exp. Stn., Ft. Collins, CO. [Unpublished]

____________________. 1985b. Net economic value of recreational steelhead fishing in Idaho. Rocky Mt. For. and Range Exp. Stn. Res. Bull. RM-9. Ft. Collins, CO. 23 pp.

Dorn, R. D. 1977. Vascular plants of Wyoming. Garland Publishing Company, New York. 1498 pp.

________. 1984. Vascular plants of Montana. Mountain West Publishing Company, Cheyenne, WY. 276 pp.

Driscoll, R. S., D. L. Merkel, D. L. Radloff, D. E. Snyder, and J. S. Hagihara. 1984. An ecological classification framework for the United States. U.S. Department of Agriculture, Forest Service Misc. Publ. 1439. 56 pp.

Driver, B. L., J. E. Bossi, and H. K. Cordell. Trends in user fees at federal outdoor recreation areas. Submitted to proceedings of trends symposium #2. [In press.]

Drury, W. H. 1956. Bog flats and physiognomic processes in the Kuskokwim River region, Alaska. Contributions of the Gray Herbarium, Harvard University, Boston. 178 pp.

Eicher, D. L. 1976. Geologic time, 2nd ed. Prentice-Hall, Inc. Englewood Cliffs, NJ. 150 pp.

Elliott, R. 1982. Faking nature. Inquiry 25:81-93.

Elliott, R., and A. Gare. 1983. Environmental philosophy, a collection of readings. Pennsylvania State University Press, University Park. 303 pp.

Ellison, L. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecol. Monogr. 24:89-104.

Enright, C. A. 1971. An analysis of mallard nesting habitat on the Monte Vista National Wildlife Refuge Colo. M.S. Thesis. Colorado State University, Fort Collins. 113 pp.

Environmental Protection Agency. 1984. Literature review of wetland evaluation methodologies. EPA Region 5, Chicago, IL. 318 pp.

Epis, R. C., and C. E. Chapin. 1975. Geomorphic and tectonic implications of the Post Laramide, Late Eocene erosion surface in the southern Rocky Mountains. Pages 45-74 in B. F. Curtis, ed. Cenozoic history of the Southern Rocky Mountains. Geol. Soc. Memoir #144.

Erman, D. C. 1976. Peat depth of Sierra Nevada fens and profile changes from 1958 to 1972 in Mason Fen. Great Basin Nat. 36:101-117.

Erman, D. C., and N. A. Erman. 1975. Macroinvertebrate composition and production in some Sierra Nevada minerotrophic peatlands. Ecology 56:591-603.

Fakey, B. 1971. A quantitative analysis of freeze-thaw cycles, frost-heave cycles, and frost penetration in the Front Range of the Rocky Mountains, Boulder County, CO. Ph.D. Dissertation. University of Colorado, Boulder. 329 pp.

Ferchau, H. 1969. Field trip log for Gunnison, Colorado area. Pages 27-48 in W. A. Weber and B. E. Willard, eds. Field Trip Number 1. XI International Botanical Congress Field Trip. August 1969.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43:421-439.

Fish, L., E. Ferstung, and J. Thomas. 1966. Stream damage surveys--1966. Resources Agency of California Fish and Game. Inland Fish. Admin. Rep. No. 66-10. University of California, Los Angeles. 16 pp.

Flint, R. F. 1971. Glacial and quaternary geology. J. Wiley and Sons, Inc., New York. 892 pp.

Flowers, S. 1934. Vegetation of the Great Salt Lakes region. Bot. Gaz. 95:353-418.

Forrest, G. I. 1971. Structure and production of North Pennine blanket bog vegetation. J. Ecol. 59:453-479.

Forrest, G. I., and R. A. H. Smith. 1975. The productivity of a range of blanket-bog types in the Northern Pennines. J. Ecol. 63:173-202.

Foster, J. H. 1979. Measuring the social value of wetland benefits. Pages 84-92 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Association, Minneapolis, MN.

Foth, H. D., and L. M. Turk. 1972. Fundamentals of soil science, S&L ed. J. Wiley and Sons, NY. 454 pp.

Frankena, W. K. 1967. Value and valuation. Pages 229-232 in Encyclopedia of philosophy, Vol. 8. MacMillan and Free Press, Riverside, NJ.

Franklin, J. F., W. H. Moir, G. W. Douglas, and C. Wiberg. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arct. Alp. Res. 3:215-224.

Friedman, R. M., and C. B. DeWitt. 1979. Wetlands as carbon and nutrient reservoirs: A spatial, historical and societal perspective. Pages 175-185 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc. Minneapolis, MN.

Fritzell, P. A. 1979. American wetlands as cultural symbol: places of wetlands in American culture. Pages 523-534 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Fuller, G. D. 1930. A comparison of certain Rocky Mountain grasslands with the prairie of Illinois. Illinois St. Acad. Sci. Trans. 8:121-130.

Gannon, P. T., J. F. Barthdic, and R. G. Bill. 1979. Climatic and meteorological effects of wetlands. Pages 576-588 in P. E. Greeson, J. R. Clark and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Geiger, R. 1959. The climate near the ground. Translation of the second German edition by Milroy N. Stewart et al. Harvard University Press, Cambridge, MA. 494 pp.

Getz, L. L. 1960. Standing crop of herbaceous vegetation in Southern Michigan. Ecology 41:393-395.

Giese, T. G. 1975. The ecology of the middle Blue River Valley, Summit County, Colorado, with an analysis of modifications due to powerline construction. M.A. Thesis. University of Colorado, Boulder. 129 pp.

Glooschenko, W. A. 1982. Sediment trace metal chemistry of Second Marsh, Ontario. Wetlands 2:207-215.

Golet, F. C., and J. S. Larson. 1974. Classification of freshwater wetlands in the glaciated Northeast. U. S. Fish Wildl. Serv. Resource Publ. 116. 56 pp.

Goodwin, R. H., and W. A. Niering. 1975. Inland wetlands of the United States. National Park Service, Natural History Theme Studies. No. 2. 549 pp.

Gore, A. J. P. 1961. Factors limiting plant growth on high-level blanket peat. I. Calcium and phosphate. J. Ecol. 49:399-402.

Gorenzel, W. P. 1979. Production, spatial, and temporal relationships of the American coot in Colorado. M.S. Thesis. Colorado State University, Fort Collins. 77 pp.

Gorenzel, W. P., R. A. Ryder, and C. E. Braun. 1981. American coot response to habitat change on a Colorado marsh. Southwest. Nat. 26:59-65.

________________. 1982. Reproduction and rest site characteristics of American coots at different elevations in Colorado. Condor 84:59-65.

Gorham, E. 1975. The relationship between standing crop in sedge meadows and summer temperature. J. Ecol. 62:487-492.

Gorham, E., and R. H. Hofstetter. 1971. Penetration of bog peats and lake sediments by tritium from atmospheric fallout. Ecology 52:898-902.

Gorham, E., and M. G. Somers. 1973. Seasonal changes in the standing crops of two montane sedges. Can. J. Bot. 51:1097-1108.

Gosselink, J. C., E. P. Odum, and R. M. Pope. 1973. The value of the tidal marsh. Center for Wetland Resources, Publ. No. LSU-SG-73-03. Louisiana State University, Baton Rouge. 31 pp.

Gosselink, J. G., and R. E. Turner. 1978. The role of hydrology in freshwater wetland ecosystems. Pages 63-78 in R. E. Good et al., eds. Freshwater wetlands: ecological processes and management potential. Academic Press, New York, NY.

Graf, W. L. 1975. The impact of suburbanization on fluvial geomorphology. Water Resour. Res. 2:690-692.

Graham, W. J., and C. A. Brown. 1983. Dam failure warnings evaluated. Natural Hazards Research and Applications Center Newsletter 7:3. University of Colorado, Boulder.

Grant, M. C., and W. M. Lewis, Jr. 1982. Chemical loading rates from precipitation in the Colorado Rockies. Tellus 34:74-88.

Grasse, J. E. 1951. Beaver ecology and management in the Rockies. J. For. 49:3-6.

Gupta, T. R., and J. H. Foster. 1975. Economic criteria for freshwater wetland policy in Massachusetts. Am. J. of Agr. Econ. 57:40-45.

Hallock D. 1985. A preliminary report on willow carrs of Boulder County. Boulder County Nature Association Publ. No. 1. Boulder, CO. 8 pp.

Hammerson, G. A., and D. Langlois. 1981. Colorado reptile and amphibian latilong study, 2nd ed. Colorado Div. of Wildlife, Denver, CO. 24 pp.

Hanson, H. C. 1929. Range resources of the San Luis Valley. Colorado Ag. Expt. Sta. Bull. No. 335. Ft. Collins, CO. 61 pp.

Harrel, R. C., and T. C. Dorris. 1968. Stream order morphometry, physicochemical conditions and community structure of benthic invertebrates in an intermittent stream system. Am. Midl. Nat. 80:220-251.

Harrington, H. D. 1954. Manual of the plants of Colorado. Sage Books, Denver, CO. 666 pp.

Harris, A. G. 1975. Geology of National parks. Kendall/Hunt Publ. Co., Dubuque, IA. 297 pp.

Harris, S. W., and W. H. Marshall. 1963. Ecology of water-level manipulation on a northern marsh. Ecology 44:331-343.

Harthill, M. P. 1968. Factors influencing the distribution of non-corticolous bryophytes in the Olympic National Park. Ph.D. Dissertation. University of Utah, Salt Lake City. 90 pp.

Haun, J. D., and H. C. Kent. 1965. Geologic history of the Rocky Mountain region. Bull. Amer. Assoc. Petrol. Geol. 49:1781-1800.

Haynes, C. M., and S. D. Aird. 1981. The distribution and habitat requirements of the wood frog (Ranidae: Rana sylvatica Le Conte) in Colorado. Colorado Div. of Wildl., Wild Res. Sect. Spec. Rept. No. 50. Denver, CO. 29 pp.

Heal, O. W., W. Flanagan, D. D. French, and S. F. MacLean, Jr. 1981. Decomposition and accumulation of organic matter. Pages 587-634 in L. C. Bliss, O. W. Heal, and J. J. Moore, eds. Tundra Ecosystem, Int'l. Biological Programme 25. Cambridge University Press. 812 pp.

Heifner, M. A. 1974. Ecological studies in Colorado alpine willow marshes. M.S. Thesis. Colorado State University, Fort Collins. 66 pp.

Heinselman, M. L. 1963. Forest sites, bog processes, and peatland types in the glacial Lake Agassiz region, Minnesota. Ecol. Monogr. 33:327-374.

_______________. 1970. Landscape evolution, peatland type, and the environment in the Lake Agassiz. Peatlands National Area, MN. Ecol. Monogr. 40:235-261.

Heliotis, F. O., and C. B. DeWitt. 1983. A conceptual model of nutrient cycling in wetlands used for wastewater treatment: a literature analysis. Wetlands 3:134-152.

Hemond, H. F. 1980. Biogeochemistry of Thoreau's Bog, Concord, MS. Ecol. Monogr. 50:507-527.

Henz, J. F., and V. R. Scheetz. 1976. The Big Thompson flood of 1976 in Colorado. Weatherwise 29(5):278-285.

Hermann, F. J. 1970. Manual of the Carices of the Rocky Mountains and Colorado Basin. USDA, Agric. Handbook No. 374. U.S. Govt. Printing Office. 397 pp.

Hess, K. 1981. Phyto-edaphic study of habitat types of the Arapahoe-Roosevelt Nat. Forest, Colorado. Ph.D. Dissertation. Colorado State University, Ft. Collins. 558 pp.

Higgins, P. D., and G. G. Spomer. 1976. Soil temperature effects on root evaporation and the ecology of alpine and subalpine plants. Bot. Gaz. 137:110-120.

Hirsch, A., and C. A. Segelquist. 1978. Position paper: protection and management of riparian ecosystems: activities and views of the U.S. Fish Wildl. Serv. Pages 353-358 in R. R. Johnson and J. F. McCormick, eds. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. USDA, For. Serv. Gen. Tech. Rep. WO-12, Washington, DC.

Hobbs, N. T., D. L. Baker, J. E. Ellis, and D. M. Swift. 1981. Composition and quality of elk winter diets in Colorado. J. Wildl. Mgmt. 45:156-171.

Hoffman, R. W. 1974. Characteristics and migration of wintering populations of Colorado white-tailed ptarmigan. M.S. Thesis. Colorado State University, Ft. Collins. 58 pp.

Hoffman, G. R., and R. R. Alexander. 1980. Forest vegetation of the Routt NF in northwestern Colorado: a habitat-type classification. USDA, For. Serv Res. Pap RM-221. Ft. Collins, CO. 41 pp.

Holch, A. E., E. W. Hertel, W. C. Oakes, and H. H. Whitwell. 1941. Root habits of certain plants of the foothills and alpine belts of Rocky Mountain National Park. Ecol. Monogr. 3:327-345.

Hulten, E. 1968. A flora of Alaska and neighboring territories: A manual of the vascular plants. Stanford University Press. Stanford, CA. 1002 pp.

Hunt, C. B. 1967. Natural regions of the United States and Canada. W. H. Freeman and Co., San Francisco, CA. 725 pp.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Ontario, Canada. 555 pp.

Ives, R. L. 1942a. A typical subalpine (or: atypical subalpine environments). Ecology 23:89-96.

__________. 1942b. The beaver meadow complex. J. Geomorph. 5:191-203.

Jarrett, R. D., and J. E. Costa. 1984. Hydrology, geomorphology, and dambreak modeling of the July 15, 1982, Lawn Lake Dam and Cascade Lake Dam Failures, Larimer County, Colorado. U.S. Geol. Surv. Open-file Rept. 84-612. 109 pp.

Jeglum, J. K. 1971. Plant indicators of pH and water level in peatlands in Candle Lake, Saskatchewan. Can. J. of Bot. 49:1661-1676.

Johnson, D. D., and A. J. Cline. 1965. Colorado mountain soils. Colorado Agric. Exper. Stat. Sci. Series Paper No. 996:233-281.

Johnson, K. R. 1941. Vegetation of some mountain lakes and shores in northwestern Colorado. Ecology 22:306-316.

Johnson, R. R., and D. A. Jones. 1977. Importance, preservation, and management of riparian habitat: a symposium. USDA, For. Serv. Gen. Tech. Rept. RM43. Rocky Mt. For. and Range Exp. Sta., Ft. Collins, CO. 218 pp.

Johnson, R. R., and J. F. McCormick. 1978. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. USDA, For. Serv. Gen. Tech. Rept. WO-12. Washington, DC. 410 pp.

Johnson, R. R., and S. W. Carothers. 1980. Riparian habitats and recreation: interrelationships and impacts in the Rocky Mountain region. Produced under agreement 53-82 FT-O-125 of the Eisenhower Consortium for Western Environmental Forestry Research, Fort Collins, CO. 109 pp.

______________. 1982. Riparian habitats and recreation: Interrelationships and impacts in the Rocky Mountain region. Eisenhower Consortium Bulletin No. 12. Rocky Mt. For. and Range Exp. Sta., Fort Collins, CO. 31 pp.

Johnson, R. S., H. L. Gary, and S. L. Ponce. 1978. Range cattle impacts on stream water quality in the Colorado Front Range. USDA, For. Serv. Res. Note. RM-359. 8 pp.

Johnston, R. S. 1984. Effect of small aspen clearcuts on water yield and water quality. USDA, For. Serv. Res. Pap. INT-333. Intermountain For. and Range Exp. Sta., Ogden, UT. 9 pp.

Johnston, R. S., and R. W. Brown. 1979. Hydrologic aspects related to the management of alpine areas. Pages 65-70 in Special management needs of alpine ecosystems. USDA, For. Serv. Gen. Tech. Rep. R672.

Kadlec, J. A. 1979. Nitrogen and phosphorus dynamics in inland freshwater wetlands. Pages 17-41 in T. A. Bookhout, ed. Waterfowl and wetlands - an integrated review. Proc. 1977 Symp., Madison, WI, The Wildlife Society.

Kadlec, R. H., and J. A. Kadlec. 1979. Wetlands and water quality (theme paper). Pages 436-456 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Keammerer, W. R. 1979. Ecology of the Keystone Bog, Keystone Mine, Colorado. Unpublished data.

Keammerer, W. R., and D. B. Keammerer. 1983. Vegetation studies on the Summitville project study area, Rio Grande County, Colorado. Unpublished report prepared for Anaconda Minerals.

Keith, L. B. 1958. Some effects of increasing soil salinity on plant communities. Can. J. Bot. 35:79-89.

Kelly, J. C., T. M. Burton, and W. R. Enslin. 1985. The effects of natural water level fluctuations on N and P cycling in a Great Lakes marsh. Wetlands 4:159-176.

Key, C. H. 1979. Mammalian utilization of floodplain habitats along the North Fork of the Flathead River in Glacier National Park. M.S. Thesis. University of Montana, Missoula. 151 pp.

Kibby, H. V. 1978. Effects of wetlands on water quality. Pages 289-298 in R. R. Johnson and J. F. McCormick, eds. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-12. Washington, DC.

Kilham, P. 1982. The biogeochemistry of bog ecosystems and the chemical ecology of Sphagnuum. Mich. Bot. 21:159-168.

Klish, M. W. 1977. The vegetation of Summit Co., CO. M.S. Thesis. Colorado State University, Ft. Collins. 103 pp.

Klotts, E. B. 1966. The new field book of freshwater life. G. P. Putnam and Sons, New York. 398 pp.

Knopf, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pages 105-111 in R. R. Johnson, C. D. Zieball, D. R. Patton, P. F. Ffolliott, and R. H. Hamre, tech. coords. Riparian ecosystems and their management: reconciling conflicting uses. USDA For. Serv. Gen. Tech. Rep. RM-120. Ft. Collins, CO.

Knopf, F. L., and R. W. Cannon. 1982. Structural resilience of a willow riparian community to changes in grazing practices. Pages 198-207 in J. M. Peek and P. D. Dalke, eds. Wildlife-livestock relationships symposium. Proceedings 10. University of Idaho, Forest, Wildlife, and Range Exp. Sta., Moscow.

Koenings, J. P. 1976. In situ experiments on the dissolved and colloidal state of iron in an acid bog lake. Limnology and Oceanography 21:674-683.

Koenings, J. P., and F. F. Hooper. 1976. Influence of colloidal organic matter on iron and iron-phosphorus cycling in an acid bog lake. Limnology and Oceanography 21:684-696.

Komarek, E. V. 1968. The nature of lightning fires. Tall Timbers Fire Ecology Conference 7:5-41.

Komarkova, V. 1979. Alpine vegetation of the Indian Peaks area, Front Range, Colorado Rocky Mountains. Flora et Fauna Mundi 7, J. Cramer, Braunschweig, 2 V., 591 pp. plus case box of tables, maps, and illustrations.

Krull, N. J. 1970. Aquatic plant macroinvertebrate associations and waterfowl. J. Wildl. Mgmt. 34:707-718.

Kuchel, C. R. 1977. Some aspects of the behavior and ecology of the harlequin ducks breeding in Glacier National Park, Montana. M.S. Thesis. University of Montana, Missoula. 169 pp.

Kuramoto, R. T., and L. C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecol. Mono. 40:317-347.

Kusler, J. A. 1983. Our National wetland heritage: A protection guidebook. An Environmental Law Institute Publication, Washington, DC. 167 pp.

Lamborn, C. R. 1962. Theoretical cross-section transect of the Blue Mesa Reservoir Basin in Colorado. University of Utah, Anthropol. Paper No. 59, 1962, Upper Colorado Series No. 8.

Langenheim, J. F. 1962. Vegetational and environmental patterns in the Crested Butte area, Gunnison Conty, Colorado. Ecol. Monogr. 32:249-285.

Latter, P. M., and J. B. Cragg. 1967. The decomposition of Juncus squarrosus leaves and microbiological changes in the profile of Juncus moor. J. Ecol. 55:465-482.

Leaf, C. F. 1975a. Watershed management in the Rocky Mountain Subalpine Zone: The status of our knowledge. USDA, For. Serv. Res. Pap. RM-137. 31 pp.

__________. 1975b. Watershed management in the Central and Southern Rocky Mountains: A summary of the status of our knowledge by vegetation types. USDA, For. Serv. Res. Pap. RM-142. 28 pp.

Leitch, W. G. 1966. Historical and ecological factors in wetland inventory. Trans. N. Am. Wildl. Nat. Resour. Conf. 31:88-96.

Leopold, A. 1949. A Sand County almanac. Oxford University Press, New York. 226 pp.

Leopold, L. B., and J. P. Miller. 1961. Ephemeral streams-hydraulic factors and their relation to the drainage net. U.S. Geol. Surv. Prof. Pap. 282A, pp. 1-38.

Leopold, L. B., and W. B. Langbein. 1966. River meanders. Sci. Am. 214:60-70.

Lesica, P. 1982. The vegetation and flora of Pine Butte Fen, Teton County, Montana. The Nature Conservancy, Helena, MT. 52 pp.

Lewis, W. M., Jr., and M. C. Grant. 1979a. Changes in the output of ions from a watershed as a result of acidification of precipitation. Ecology 60:1093-1097.

____________________. 1979b. Relationships between stream discharge and yield of dissolved substances from a Colorado mountain watershed. Soil Sci. 128:353-363.

____________________. 1980. Relationships between snow cover and winter losses of dissolved substances from a mountain watershed. Arct. Alp. Res. 12:11-17.

____________________. 1984. Chemical patterns of bulk atmospheric deposition in the State of Colorado. Water Resour. Res. 20:1691-1704.

Likens, G. E., F. H. Bormann, and N. M. Johnson. 1972. Acid rain. Environment 14:33-40.

Likens, G. E., and F. H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. Bioscience 24:447-456.

Lippert B. E., and D. L. Jameson. 1964. Plant succession in temporary ponds of the Willamette Valley, Oregon. Am. Midl. Nat. 71:181-197.

Livingston, R. J., and O. L. Loucks. 1979. Productivity, trophic interactions, and food-web relationships in wetlands and associated systems. Pages 101-119 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Loach, K. 1968. Relations between soil nutrients and vegetation in wet-heaths. II. Nutrient uptake by the major species in the field and in controlled conditions. J. Ecol. 56:117-127.

Longwell, C. R., A. Knopf, and R. F. Flint. 1939. A textbook of geology, Part I-physical geology. J. Wiley & Sons, Inc., New York. 543 pp.

Loomis, J. B. 1986. Importance of net economic values of wildlife planning and impact assessment. In R. Comer, ed. Issues and technology in the management of impacted western wildlife, No. II. Proceedings of a National Symposium, Glenwood Springs, CO. February, 1985. Thorne Ecological Inst., Boulder, CO. [In press.]

Loomis, J. B, G. Peterson, and C. Sorg. 1985. A field guide to wildlife economic analyses. Pages 315-324 in K. Sabol, ed., Proceedings of 49th North American Wildlife and Natural Resources Conference, Wildlife Management Institute.

MacLean, S. F., Jr. 1981. Introduction: Invertebrates. Pages 377-396 in L. C. Bliss, O. W. Heal, and J. J. Moore, eds. Tundra Ecosystems. Intl. Biological Programme No. 25, Cambridge University Press, Cambridge, England.

Maguire, L. A. 1974. A model of beaver population and feeding dynamics in a peatland at Houghton Lake, Michigan. M.S. Thesis. University of Michigan, Ann Arbor. 127 pp.

Mannison, D. 1983. Nature may be of no value. A reply to Elliott. Inquiry 26:233-235.

Manny, B. A., R. G. Wetzel, and W. C. Johnson. 1975. Annual contributions of carbon, nitrogen, and phosphorus by migrant Canada geese to a hardwater lake. Intl. Verein. Theoret. Aug. Limnol. Verh. 19:949-951.

Marr, J. 1967. Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies, Ser. Biology No. 8. University of Colorado Press, Boulder. 134 pp.

Marrinucci, A. C., J. E. Hobbie, and J. V. K. Helfrich. 1983. Effect of litter nitrogen on decomposition and microbial biomass in Spartina alternaflora. Microbial Ecology 9:27-40.

Martin, W. C., and C. R. Hutchins. 1981. Flora of New Mexico. J. Cramer Publ., Vaduz. Switz. 2 vol., 2591 pp. plus 1300 maps and 435 illustrations.

Mathis, B. J. 1967. Species diversity of benthic macroinvertebrates in three mountain streams. Trans. Ill. Acad. Sci. 171-176.

Matsumura Y., and H. D. Harrington. 1955. The true aquatic vascular plants of Colorado. Colo. A & M Tech. Bull. 57. 130 pp.

Matthes, F. 1900. Glacial sculpture of the Big Horn Mountains, Wyoming. U.S. Geological Surv. 21st Ann. Rept. 1899-1900:173-190.

Mauk, R. L., and J. A. Henderson. 1984. Coniferous forest habitat types of Northern Utah. USDA For. Serv., Gen. Tech. Rept. INT-170. Ogden, UT. 89 pp.

May, T. A. 1970. Seasonal foods of white-tailed ptarmigan in Colorado. M.S. Thesis. Colorado State University, Ft. Collins. 55 pp.

McCalpin, J. 1981. Quaternary geology and neotectonics of the west flank of the northern Sangre de Cristo Mountains, Southcentral Colorado. Ph.D. Dissertation. Colorado School of Mines, Golden. 287 pp.

McClelland, B. R. 1973. Autumn concentrations of bald eagles in Glacier National Park. Condor 75:121-123.

_____________. 1981. Management of people at the autumn concentrations of bald eagles in Glacier National Park. Proc. Bald Eagle Days 1981. pp. 237-240.

McColl, J. W., and J. Burger. 1975. Chemical inputs by a colony of Franklin's gulls nesting in cattails. Am. Midl. Nat. 96:270-280.

McCorkle, C. O., Jr., and J. E. Halver. 1982. Impacts of emerging agricultural trends on fish and wildlife habitat. National Research Council. National Academy Press, Washington, DC. 303 pp.

McGarity, J. W. 1962. Effect of freezing of soil on denitrification. Nature 196:1342-1343.

McLeod, W. K., and J. K. McPherson. 1973. Factors limiting the distribution of *Salix nigra*. Bull. Torr. Bot. Club 100:102-110.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59:465-472.

Meier, M. F. 1961. Distribution and variations of glaciers in the United States exclusive of Alaska. Inter. Assoc. Sci. Hydrol. Publ. 54:420-429.

Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621-626.

Menke, J., ed. 1977. Symposium on livestock interaction with wildlife, fisheries and their environments. Sparks, NV. USDA For. Serv., Pacific Southwest For. and Range Exp. Stn., Berkeley, CA.

Merriam, C. H. 1890. San Francisco Mountains. USDA, N. Amer. Fauna 3:1-136.

_____________. 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. National Geographic Magazine. 6:229-238.

_____________. 1898. Life zones and crop zones of the United States. USDA, Div. Biol. Surv. Bull. 10:1-79.

Merritt, R. W., and K. W. Cummins. 1984. An introduction to the aquatic insects of North America, 2nd ed. Kendall/Hunt Publishing Company, Dubuque, IA. 722 pp.

Millar, J. B. 1973. Vegetation changes in shallow marsh wetlands under improving moisture regime. Can. J. Bot. 51:1445-1457.

__________. 1976. Wetland classification in western Canada: A guide to marshes and shallow open water wetlands in grasslands and parklands of the prairie province. Can. Wildl. Serv. Rep. Ser. 37. 38 pp.

Miller, P. C. 1964. Factors influencing the vegetation pattern on the White River Plateau in northwestern Colorado. Ph.D. Thesis. University of Colorado, Boulder. 208 pp.

Minnesota Department of Natural Resources. 1980. Trout streams in southeastern Minnesota. St. Paul. 373 pp.

Molles, M. C. 1980. Effects of road salting on aquatic invertebrate communities. Eisenhower Consortium Bulletin 10. Rocky Mt. For. and Range Exp. Sta., Fort Collins, CO. 9 pp.

Moore, P. D., and P. D. Bellamy. 1974. Peatlands. Springer-Verlag, New York. 222 pp.

Morris, D. P. 1985. Nutrient limitation of phytoplankton in selected Colorado lakes. M.S. Thesis. University of Colorado, Boulder. 87 pp.

Moss, E. H. 1955. The vegetation of Alberta. Bot. Rev. 21:493-567.

Mueggler, W. F., and C. A. Harris. 1969. Some vegetation and soil characteristics of mountain grasslands in Central Idaho. Ecology 50:671-678.

Mueggler, W. F., and W. L. Stewart. 1980. Grassland and shrubland habitat types of Western Montana. USDA, For. Serv. Gen. Tech. Rept. INT-66. Ogden, UT. 154 pp.

Mutel, C. F. 1973. An ecological study of the plant communities of certain montane meadows in the Front Range of Colorado. M.A. Thesis. University of Colorado, Boulder. 77 p.

Mutz, K. M., and R. Graham. 1982. Riparian community type classification. Big Piney, Wyoming, Ranger Dist. 88 pp.

Nash, R. 1982. Wilderness and the American mind, 3rd ed. Yale University Press, New Haven, CT. 425 pp.

Neff, D. J. 1957. Ecological effects of beaver habitat abandonment in the Colorado Rockies. J. Wildl. Mgt. 21:80-84.

Nelson, N. F. 1955. Ecology of Great Salt Lake marshes. Utah Acad. of Sci., Arts and Letters 32:37-40.

Nelson, N. F., and R. H. Dietz. 1966. Cattail control methods in Utah. Utah State Dept. of Fish and Game. Pub. No. 66-2, Fed. Aid Proj. W-29-R.

Nelson, R. A. 1970. Plants of Rocky Mountain National Park. Rocky Mtn. Nat. Assn., Estes Park, CO. 168 pp.

Nichols, D. S. 1983. Capacity of natural wetlands to remove nutrients from wastewater. J. Water Poll. Contr. Fed. 55:495-505.

Nicholson, S. A., and B. Aroyo. 1975. A case study of hydrarch zonation. Vegetation 30:207-212.

Niering, W. 1979. Our wetland heritage. Historic, artistic and future perspectives. Pages 505-522 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Noble, D. L., and M. Howe. 1983. Cyanide in riparian vegetation. Pages 498-505, in Proceedings of symposium on gold, silver, uranium, and coal geology, mining, extraction, and the environment. Rapid City, SD. 1980.

Norton, B. E. 1981. Riparian community classification for the Greys River, Wyoming. Unpubl. Rept. USDA For. Serv. Region IV. Dept. of Range Sci., Utah State University, Logan. 190 pp.

Novitzki, R. P. 1978. The hydrologic characteristics of Wisconsin's wetlands and their influence on floods, streamflow, and sediment. Pages 377-388 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetlands functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Nowlin, R. A. 1985. Distribution of moose during occupation of vacant habitat in northcentral Colorado. Ph.D. Thesis. Colorado State University, Ft. Collins. 60 p.

Odum, E. P. 1971. Fundamentals of ecology, 3rd ed. W. B. Saunders Co., Philadelphia. 574 pp.

__________. 1978. Ecological importance of the riparian zone. Pages 2-4 in R. R. Johnson and J. F. McCormick, tech. coords. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. USDA, For. Serv. Gen. Tech. Rept. WO-12, Washington, DC.

__________. 1979. The value of wetlands: a hierarchical approach. Pages 16-24 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Odum, E. P., and H. T. Odum. 1972. Natural areas as necessary components of man's total environment. Trans. North Amer. Wildl. and Nat. Res. Conf. 37:178-189.

Odum, H. T., B. J. Copeland, and E. A. McMahon, eds. 1974. Coastal ecological systems of the United States. The Conservation Foundation, Washington, DC.

Odum, H. T., W. Kemp, M. Sell, W. Boynton, and M. Lehman. 1977. Energy analysis and the coupling of man and estuaries. Env. Manage. 1:297-315.

Odum, W. E., T. J. Smith, III, J. K. Hoover, and C. C. McIvor. 1984. The ecology of tidal freshwater marshes of the United States East Coast: a community profile. FWS/OBS-83/17. 177 pp.

Oetking, P., D. E. Feray, and H. B. Renfro. 1967. Geological highway map: Southern Rocky Mountain Region, Utah-Colorado, Arizona-New Mexico. American Society of Petroleum Geologists, Tulsa, OK.

Office of Technology Assessment. 1984. Wetlands: their use and regulation. OTA-0206. Washington, DC. 208 pp.

Onuf, C. P., J. M. Teal, and I. Valiela. 1977. Interaction of nutrients, plant growth, and herbivores in a mangrove system. Ecology 58:514-526.

Oosting, H. J. 1956. The study of plant communities: An introduction to plant ecology, 2nd ed. Freeman Inc., New York. 440 pp.

Oppenheimer, M., C. B. Epstein, and R. E. Yuhnke. 1985. Acid deposition, smelter emissions, and the linearity issue in the Western United States. Science 229:859-862.

Osburn, W. S., Jr. 1963. The dynamics of fallout distribution in Colorado alpine tundra snow accumulation ecosystems. Pages 51-71 in V. Schultz and A. W. Klement, Jr., eds. Radioecology. 746 pp.

______________. 1969. Accountability of nuclear fallout deposited in a Colorado high mountain bog. Pages 578-586 in D. J. Nelson and F. C. Evans, eds. Symposium on radioecology. U.S. Atomic Energy Comm., Conf. 670503.

Ostler, W. K., K. T. Harper, K. B. McKnight, D. C. Anderson. 1982. The effects of increasing snowpack on a subalpine meadow in the Uinta Mountains, Utah, U.S.A. Arct. Alp. Res. 14:203-214.

Owens, T. 1980. Alpine wetlands in Colorado. Colorado State Forest Service. 17 pp. [Unpublished paper.]

Paavilainen, E. 1974. The use of nitrogen in fertilizing peatland forests. Pages 337-345 in Proceedings of international symposium on forest drainage. Jyvaskyla-Oulu, Finland.

Panek, F. M. 1979. Cumulative effects of small modifications to habitat. Fisheries 4:54-57.

Patten, D. T. 1963. Vegetational pattern in relation to environments in the Madison Range, Montana. Ecol. Mono. 33:375-406.

Pearsall, W. H. 1920. The aquatic vegetation of English lakes. J. Ecol. 8:163-201.

______________. 1929. Dynamic factors affecting aquatic vegetation. Proc. Intl. Congr. Plant Sci., pp. 667-672. Ithaca, NY, August 1926.

Pearsall, W. H., and E. Gorham. 1956. Production ecology. I. Standing crop of natural vegetation. Oikos 7:193-201.

Pearsall, W. H., and P. J. Newbould. 1957. Production ecology IV. Standing crops of natural vegetation in the subarctic. J. Ecol. 45:593-599.

Pederson, R. L., and A. G. Van der Valk. 1984. Vegetation change and seed banks in marshes: ecological and management implications. Trans. N. Am. Wild. & Natur. Res. Conf. 49:271-280.

Penfound, W. T. 1953. Plant communities in Oklahoma lakes. Ecology 34:561-583.

Pennak, R. W. 1963. Ecological and radiocarbon correlations in some Colorado lake and bog deposits. Ecology 44:1-15.

__________. 1978. Fresh-water invertebrates of the United States, 2nd ed. J. Wiley and Sons, New York. 803 pp.

Peterson, G. L. 1985. Economic growth from forest-based recreation, wildlife and tourism. Paper presented at the 1985 Forestry and Wildlife Forum, April 12. Blackburg, VA.

Peterson, G. L., and A. Randall. 1984. Valuation of wildland resource benefits. Westview Press, Boulder, CO. 258 pp.

Peterson, R. T. 1941. A field guide to western birds. Houghton Mifflin Co., Boston, MA. 240 pp.

Phillips, C. M. 1977. Willow carrs of the Upper Laramie River Valley, Colorado. M.S. Thesis. Colorado State University, Ft. Collins, CO. 71 pp.

Pierce, J. R. 1982. A floristic study of the Big Hole National Battlefield. M. A. Thesis. University of Montana, Missoula. 265 pp.

Platts, W. S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. Fisheries 4:5-9.

__________. 1981. Effects of sheep grazing on a riparian-stream environment. USDA, For. Serv. Res. Note INT-308. Ogden, UT. 6 pp.

Ploskey, G. R., and R. M. Jenkins. 1980. Inventory of U.S. Reservoirs. USDI, FWS, National Reservoir Research Program. Mimeo Rept. 20 pp.

Posphala, R. S. 1969. Waterfowl production and vegetative response to early water. M.S. Thesis. Colorado State University, Ft. Collins. 96 pp.

Price, L. W. 1981. Mountains and man. A study of processes and environment. University of California Press, Los Angeles. 506 pp.

Quinlan, R. E. 1980. A study of the biology of the Colorado cutthroat trout (*Salmo clarki pleuriticus*) population in the North Fork of the Little Snake River drainage in Wyoming. M.A. Thesis. University of Wyoming, Laramie.

Ramaley, F. 1919. The role of sedges in some Colorado plant communities. Am. J. Bot. 6:120-130.

_________. 1920. Subalpine lake shore vegetation in north-central Colorado. Am. J. Bot. 7:57-74.

_________. 1942. Vegetation of the San Luis Valley in Southern Colorado Univ. of Colorado Stud. Ser. D. Phys. and Biol. Sci. 1:231-277.

Ramaley, F., and W. W. Robbins. 1909. Studies in lake and streamside vegetation I. Redrock Lake near Ward, Colorado. University of Colorado Stud. 6:131-168.

Reader, R. J., and J. M. Stewart. 1972. The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. Ecology 53:1024-1037.

Ream, R. R. 1963. The vegetation of the Wasatch Mountains, Utah and Idaho. Ph.D. Dissertation. University of Wisconsin, Madison.

Reed, E. L. 1917. Meadow vegetation in the montane region of Northern Colorado. Torrey Bot. Club Bull. 44:97-109.

Reed, J. F. 1952. The vegetation of the Jackson Hole Wildlife Park, Wyoming. Am. Midl. Nat. 48:700-729.

Reed, P. B., Jr. 1986. Wetland plants of the United States of America 1986. U.S. Fish Wildl. Serv., Western Energy and Land Use Team, Ft. Collins, CO. WELUT-86/W17.01.

Reid, W. H. 1972. Analysis of plant ecological systems through simulation of individual organisms. Ph.D. Dissertation. University of Colorado, Boulder. 265 pp.

Reimold, R. J., and M. A. Hardisky. 1979. Nonconsumptive use values of wetlands. Pages 558-562 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Retzer, J. L. 1956. Alpine soils of the Rocky Mountains. J. Soil Sci. 7:22-32.

_________. 1962. Soil survey of the Fraser alpine area, Colorado. U.S. Dept. Agr. in cooperation with the Colorado Agric. Exp. Station, U.S. Forest Service, and Soil Conserv. Serv. Ser. 1956, #20, pp. 1-47.

Richardson, G. J. 1979. Primary productivity values in fresh water wetlands. Pages 131-145 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

______________. 1985. Mechanisms controlling phosphorous retention capacity in freshwater wetlands. Science 228:1424-1427.

Richmond, G. M. 1960. Glaciation of the east slope of Rocky Mountain National Park, Colorado. Geol. Soc. Amer. Bull. 71:1371-82.

Riggs, R. A., and C. Armour. 1978. A hypothesis for predicting grizzly bear habitat use in spring floodplain habitat mosaics with special reference to reducing human-bear contact rates. Glacier National Park, MT. 28 pp. [Unpubl. Rept.]

Robbins, W. W. 1910. Climatology and vegetation in Colorado. Bot. Gaz. 49:256-280.

______________. 1918. Successions of vegetation in Boulder Park, Colorado. Bot. Gaz. 65:493-525.

Robinson, G. G. W. 1971. Vegetation and physical factors influencing waterfowl production. M.S. Thesis. Colorado State University, Ft. Collins. 148 pp.

Rolston, H., III. 1981. Values in nature. Env. Ethics 3:111-128.

______________. 1982. Are values in nature subjective or objective? Env. Ethics 4:125-151.

Rosenthal, D. H., J. B. Loomis, and G. L. Peterson. 1984. The travel cost model: concepts and applications. USDA For. Serv. Gen. Tech. Rep. RM-109. Fort Collins, CO. 10 pp.

Rosine, W. N. 1955a. The distribution of invertebrates on submerged aquatic plant surface in Muskee Lake, Colorado. Ecology 36:308-314.

______________. 1955b. Wildlife and environmental relationships of beavers in Colorado forests. J. For. 53:803-806.

Routley, R., and V. Routley. 1979. Against the inevitability of human chauvinism. Pages 36-59 in K. E. Goodpaster and K. M. Sayre, eds. Ethics and problems of the 21st century. University of Notre Dame Press, Notre Dame, IN.

Ryder, R. A. 1951. Waterfowl production in the San Luis Valley, Colorado. M.S. Thesis. Colorado State University, Ft. Collins. 166 pp.

Ryther, J. H., et al. 1979. Freshwater macrophytes for energy and waste water treatment. Pages 652-660 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Salwasser, H., R. H. Barrett, and C. Sorg. 1984. Fish and wildlife values: new clout for a conservation ethic. Cal-Neva Wildl. Trans. [In press.]

Sands, A., ed. 1980. Riparian forests in California--their ecology and conservation. Proc. of the Symp. Div. of Agric. Sci., University of California, Berkeley. 122 pp.

Sarnecki, J. C. 1983. Selected trace elements anomalies in a Front Range bog, Larimer County, Colorado. In R. Raymond, Jr. and M. J. Andrejko, eds. Proceedings of workshop in mineral matter in peat: its occurrence, form, and distribution. Los Alamos National Laboratory, Los Alamos, NM.

Sather, J. H., and R. H. Smith. 1984. An overview of major wetland functions and values. FWS/OBS-84/18. 100 pp.

Sather, J. H., and P. J. Stuber. 1984. Proceedings of the National wetlands assessment workshop. FWS/OBS-84/12. 100 pp.

Schaffer, S. 1971. Some ecological aspects of grizzly bears and black bears in Glacier National Park. M.S. Thesis. University of Montana, Missoula. 134 pp.

Schiemer, F., and M. Prosser. 1976. Distribution and biomass of submerged macrophytes in Neusiedlersee. Aq. Botany 2:289-307.

Schlatterer, E. F. 1972. A preliminary description of plant communities found on the Sawtooth, White Cloud, Boulder and Pioneer Mountains. USDA, For. Serv. Int. Mt. Reg. 111 pp.

Schwintzer, C. R. 1978. Vegetation and nutrient status of Northern Michigan fens. Can. J. Bot. 56:3044-3051.

Sexton, O. J., and J. R. Bizer. 1978. Life history patterns of Ambystona tigrinuum in montane Colorado. Amer. Midl. Nat. 99:101-118.

Shaw, S. P., and C. G. Fredine. 1956. Wetlands of the United States: Their extent and their value to waterfowl and other wildlife. U.S. Fish and Wildlife Service, Circular 39. 67 pp.

Shea, D. S. 1978. Bald eagle concentrations in Glacier National Park. Western Birds 9:35-37.

Shelford, V. E. 1907. Preliminary notes on the distribution of the tiger beetle (Cicindelae) and its relation to plant succession. Biol. Bull. 14:9-14.

________________. 1911. Ecological succession. I. Stream fishes and the method of physiographic analysis. Biol. Bull. 21:9-34.

Shulls, W. A. 1982. A review of some aspects of bacterial decomposition of plant litter in the Colorado alpine. Inst. Arct. Alp. Res. University of Colorado, Boulder. Occasional Paper No. 37. 138-147.

Shute, D. A. 1981. Classification and ecology of Salix (willow) communities in southwestern Wyoming. J. Colo.-Wyo. Acad. Sci. 13:15. [Abstract]

Silberhorn, G. M., G. M. Dawes, and T. A. Barnard. 1974. Coastal wetlands of Virginia. Virginia Inst. of Marine Sci. Gloucester Point, VA. 54 pp.

Simpson, P. W., J. R. Newman, M. A. Keirn, R. M. Matter, and P. A. Guthrie. 1982. Manual of stream channelization impacts on fish and wildlife. FWS/OBS-82/24. 155 pp.

Singer, F. J. 1978. Seasonal concentrations of grizzly bears, North Fork of Flathead River, Montana. Can. Field Nat. 82:283-286.

Sjors, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2:241-258.

________. 1959. Bogs and fens in the Hudson Bay Lowlands. Arctic 12:2-19.

________. 1961. Surface patterns in boreal peatlands. Endeavor 20:217-224.

________. 1965. Regional ecology of mire sites and vegetation in the plant cover of Sweden. Acta Phyto Suec 50:180-188.

Slack, N. G., D. H. Vitt, and D. G. Norton. 1980. Vegetation gradients of minerotrophically rich fens in Western Alberta. Can. J. Bot. 58:330-350.

Small, E. 1972. Ecological significance of four critical elements in plants of raised Sphagnum peat bogs. Ecology 53:498-503.

Smarlson, R. C. 1979. Visual-cultural values of wetlands. Pages 535-544, in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Soil Survey Staff. 1975. Soil taxonomy. Soil Conservation Service, USDA, Handbook No. 439.

Sorg, C. F., and J. B. Loomis. 1984. Empirical estimates of amenity forest values: a comparative review. USDA For. Serv. Gen. Tech. Rep. RM-107. Ft. Collins, CO. 23 pp.

Sorg, C. F., and J. B. Loomis. 1985. An introduction to wildlife valuation techniques. Wildl. Soc. Bull. 13:38-46.

Sorg, C. F., D. M. Donnelly, J. B. Loomis, and G. L. Peterson. 1984. Implications of economics as applied to wild trout fisheries management in Idaho. Paper presented at the Wild Trout III symposium, Mammoth, WY, Yellowstone National Park, Sept. 24-25.

Sparling, J. H. 1966. Studies on the relationship between water movement and water chemistry in mires. Can. J. Bot. 44:747-758.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the Central Rocky Mountains. Ecology 24:19-30.

Starr, C. R. 1974. Subalpine meadow vegetation in relation to environment at Headquarter Park, Medicine Bow Mountains, Wyoming. M.S. Thesis. University of Wyoming, Laramie. 94 pp.

Steele, R., R. D. Pfister, R. A. Ryker, and J. A. Kittans. 1981. Forest habitat types of central Idaho. USDA, For. Serv. Gen. Tech. Rept. INT-114. Ogden, UT. 138 pp.

Steele, R., S. V. Cooper, D. M. Ondov, D. W. Roberts, and R. D. Pfister. 1983. Forest habitat types of Eastern Idaho - Western Wyoming. USDA, For. Serv. Gen. Tech. Rept. INT-144. Ogden, UT. 122 pp.

Stewart, B. K. 1940. Plant ecology and paleoecology of the Creede Valley, Colorado. Ph. D. Thesis. University of Colorado, Boulder. 154 pp.

Stewart, R. E., and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Fish Wildl. Serv. Resour. Publ. 92. 57 pp.

Stuber, R. 1985. U.S. Forest Service, Ft. Collins, Colorado. Personal communication.

Sturges, D. L. 1967. Water quality as affected by a Wyoming mountain bog. Water Resour. Res. 3:1085-1089.

____________. 1968. Hydrologic properties of peat from a Wyoming mountain bog. Soil Sci. 106:262-264.

Sturges, D. L., and R. E. Sundin. 1968. Gross alpha and beta radiation in waters in a Wyoming bog. Water Resour. Res. 4:159-162.

Swanson, G. A., tech. coord. 1979. The mitigation symposium: a national workshop on mitigating losses of fish and wildlife habitats. USDA, For. Serv. Gen. Tech. Rep. RM-65. Ft. Collins, CO. 684 pp.

Swift, B. L. 1984. Status of riparian ecosystems in the United States. Water Resources Bull. 20:223-228.

Swift, B. L., and J. S. Barclay. 1980. Status of riparian ecosystems in the United States. Paper presented at the 1980 American Water Resources Assn. Natl. Conf. Minneapolis, MN. 29 pp.

Szilagy, M. 1973. The redox properties and the determination of the mammal potential of the peatwater system. Soil Sci. 115:434-437.

Tansley, A. G. 1939. The British Islands and their vegetation. Cambridge University Press, Cambridge, England. 930 pp.

Taylor, P. W. 1981. Respect for nature. Env. Ethics 3:197-218.

Tchonbanoglous, G., and G. L. Culp. 1980. Wetland systems of wastewater treatments: an engineering assessment. Pages 12-42 <u>in</u> aquaculture systems for wastewater treatment: an engineering assessment. U.S. Environmental Protection Agency McD 68 EPA 43019-80-07. Washington, DC.

Thomas, J. W., C. Maser, and J. E. Rodiek. 1979. Habitats in managed rangelands -- the Great Basin of Southeastern Oregon -- riparian zones. USDA, For. Serv. Gen. Tech. Rep. PNW-80. La Grande, OR. 18 pp.

Thornbury, W. D. 1965. Regional geomorphology of the United States. John Wiley and Sons, Inc., NY. 609 pp.

Thornthwaite, C. W. 1931. The climates of North America according to a new classification. Geog. Rev. 21:633-655.

Thurman, E. M. 1985. Organic geochemistry of natural waters. Maritimes Nyhoff/Dr. W. Junk Publishers, Boston, MA. 487 pp.

Tilton, D. L., and B. R. Schweiger. 1979. The values of wetland habitat in the Great Lakes basin. Pages 267-277 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Tiner, R. W. 1984. Wetlands of the United States: current status and recent trends. U.S. Dept. of the Interior, Fish and Wildlife Service. 59 pp.

Torres, J., S. Bissel, G. Craig, W. Graul, and D. Langlois. 1978. Essential habitat for threatened or endangered wildlife in Colorado. Colorado Dept. of Wildlife Publ. Denver. 84 pp.

Transeau, E. N. 1903. On the geographical distribution and ecological relationships of the bog societies of North America. Bot. Gaz. 36:401-421.

Trewartha, G. T. 1943. An introduction to weather and climate, 2nd ed. McGraw-Hill Book Co., New York. 545 pp.

Ungar, I. A. 1974. Halophyte communities of Park County, Colorado Bull. Torr. Bot. Club. 101:145-152.

U.S. Department of Agriculture, Soil Conservation Service. 1975. Soil Taxonomy, Agriculture Handbook #436. 754 pp.

________________. 1978. Range site descriptions for Colorado. Tech. guide section II-E, Colorado State Office, Denver, CO. (Uncompiled and unnumbered).

________________. 1980. An assessment of the forest and range land situation in the United States. U.S. For. Serv. FS-345. Washington, DC. 631 pp.

U.S. Department of Commerce, National Weather Service. 1976. Daily weather maps--weekly series, 31 July, 1976. Superintendent of Documents, Government Printing Office, Washington, DC 20402.

________________. 1981. Daily weather maps--weekly series, 27 Dec., 1981. Superintendent of Documents, Government Printing Office, Washington, DC 20402.

________________. 1985. Daily weather maps--weekly series, 3 March, 1985. Superintendent of Documents, Government Printing Office, Washington, DC 20402.

U.S. Department of the Interior. 1955. Wetland inventory Colorado: field work and report by the Office of River Basin Studies, Region 2. U.S. Fish and Wildlife Service, Albuquerque, NM.

________________. 1982. 1980 National survey of fishing, hunting, and wildlife-associated recreation. U.S. Dept. of the Interior, Fish and Wildl. Serv., and U.S. Dept. of Commerce, Bureau of Census. 156 pp.

U.S. Department of the Interior, Bureau of Land Management. 1967. Range condition report. Prepared for U.S. Senate Committee on Appropriations. Govt. Printing Office. Washington, DC. 620 pp.

U.S. Department of the Interior, Bureau of Land Management. 1979a. Manual section 6610: Terrestrial wildlife riparian habitat inventory.

________________. 1979b. Manual section 6740: Wetland-riparian area protection and management. 12 pp.

U.S. Department of the Interior, Fish and Wildlife Service. 1984. Endangered and threatened wildlife and plants. 50 CFR 17.11 and 17.12. U.S. Government Printing Office. 19840-447-430. 24 pp.

U.S. Department of the Interior, Geological Survey. 1970. The national atlas of the United States of America. Washington, DC. 417 pp.

________________. 1973. Glaciers: A water resource. GPO:0-508-949, Washington, DC. 8 pp.

________________. 1974. Mimeographed report. Denver, CO.

________________. 1983. Monthly discharge of Big Thompson River. Denver, CO.

U.S. Fish and Wildlife Service, National Wetland Inventory. 1981. Mapping conventions for the National Wetland Inventory. St. Petersburg, FL. 26 pp (mimeo).

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology 62:688-696.

________________. 1982. Succession in temperate North American wetlands. Pages 10-17 _in_ B. Gopal et al., eds. Wetlands ecology and management. Proceedings _of_ First Intl. Wetlands Conf. New Delhi, India, Sept. 1980. Lucknow Pub. House, Lucknow, India.

van der Valk, A. G., and L. C. Bliss. 1971. Hydrarch succession and net primary production of oxbow lakes in Central Alberta. Can. J Bot. 49:1177-1199.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:370-379.

Verry, E. S. 1975. Stream flow chemistry and nutrient yields from upland peatland watersheds in Minnesota. Ecology 56:1149-1157.

Verry, E. S., and D. H. Boelter. 1978. Peatland hydrology. Pages 389-402 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Vestal, A. G. 1914. Foothills vegetation in the Colorado Front Range. Bot. Gaz. 58:377-400.

Viereck, L. A. 1970. Forest succession and soil development adjacent to the Chena River in interior Alaska. Arct. Alp. Res. 2:1-26.

Voights, D. K. 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. Am. Midl. Naturalist 95:313-322.

Walker, D. 1970. Direction and rate in some British post-glacial hydroseres. Pages 117-139 in D. Walker and R. G. West, eds. Studies in the vegetational history of the British Isles. Cambridge University Press, Cambridge, England. 266 pp.

Walsh, R. G., R. D. Bjonback, D. H. Rosenthal, and R. A. Aiken. 1986. Public benefits of programs to protect endangered wildlife in Colorado. In R. Comer, ed. Issues and technology in the management of impacted western wildlife, No. II. Glenwood Springs, CO, February, 1985. Thorne Ecological Inst., Boulder, CO. [In press.]

Walters, M. A., R. O. Teskey, and T. M. Hinckley. 1980. Impact of water level changes on woody riparian and wetland communities. Volume VIII: Pacific Northwest and Rocky Mountain Regions. U.S. Fish Wildl. Serv. FWS/OBS-78/94. 46 pp.

Ward, J. V. 1985. An illustrated guide to the mountain stream insects of Colorado. Colorado State University, Ft. Collins. 199 pp.

Warner, R. E., recorder. 1979. Fish and wildlife resource needs in riparian ecosystems. Proc. of a workshop. May 30-31, 1979, Harpers Ferry, WV. National Water Resources Analysis Group. Eastern Energy and Land Use Team. U.S. Fish and Wildlife Service, Kearneysville, WV. 53 pp.

Warner, R. E. 1980. California riparian study program, California Fish and Game Rept. Rangelands 2:165-167.

Watt, R. F., and M. L. Heinselman. 1976. Foliar nitrogen and phosphorus level related to site quality in a northern Minnesota spruce bog. Ecology 46:357-361.

Weaver, J. E., and F. E. Clements. 1938. Plant ecology. McGraw-Hill Book Company, Inc., New York. 520 pp.

Weber, W. A. 1965. Plant geography in the southern Rocky Mountains. Pages 453-468 in H. E. Wright and D. G. Frey, eds. The Quaternary of the U.S. Princeton University Press, Princeton, NJ.

__________. 1976. Rocky Mountain flora. Colorado University Press, Boulder. 479 pp.

Welch, S. L. 1973. Utah plants. Brigham Young University Press, Provo, UT. 474 pp.

Western Land Grant Universities and Colleges. 1964. Soils of the Western United States. Washington State University, Pullman. 69 pp.

Wetzel, R. G. 1983. Limnology. W. B. Saunders Co., New York. 762 pp.

Whigham, D. F., and S. E. Bayley. 1979. Nutrient dynamics in freshwater wetlands. Pages 468-478 in P. E. Greeson, J. R. Clark, and J. E. Clark, eds. Wetland functions and values: the state of our understanding. Am. Water Resour. Assoc., Minneapolis, MN.

Wilcox, D. A., S. I. Apfelbaum, and R. D. Hiebert. 1985. Cattail invasion of sedge meadows following hydrologic disturbance in the Cowles Bog Wetland Complex, Indiana Dunes National Lakeshore. Wetlands 4:115-128.

Willard, B. E. 1979. Plant sociology of alpine tundra, Trail Ridge, Rocky Mountain National Park, Colorado. Colorado School of Mines Qtly. 74:1-119.

__________. 1985. Inventory of some wetlands in Rocky Mountain National Park. [Unpublished ms. 17 June 1985.]

Willard, B. E., E. D. A. Aisibey, M. W. Holdgate, Y. Furushima, E. Dodson Gray, and D. Dodson Gray. 1980. Ethics of biospheral survival: a dialogue. Pages 505-551 in N. Polunin, ed. Growth without ecodisasters. Proceedings of the second international conference on environmental future (2nd ICEF) Reykjavik, Iceland, June 1977.

Willard, B. E., and J. W. Marr. 1960. Investigations on effects of visitor use on ecosystems of Rocky Mountain National Park, Colorado I. Unpublished report for National Park Service. USDI Washington, DC. 31 pp.

__________. 1961. Investigations on effects of visitor use on ecosystems of Rocky Mountain National Park, Colorado II. Unpublished report for National Park Service, USDI. Washington, DC. 64 pp.

Willard, L. D. 1980. On preserving nature's aesthetic features. Env. Ethics 2:293-310.

Wilson, H. C. 1969. Ecology and successional patterns of wet meadows, Rocky Mountain National Park, Colorado. Ph.D. Thesis. University of Utah, Salt Lake City. 99 pp.

Wilson, J. T., compiler. 1970. Continents adrift - readings from Scientific American. W. H. Freeman and Co., San Francisco, CA. 172 pp.

Windell, J. T., and S. Q. Foster. 1982. The status of unexploited fish populations in the Green Lakes Valley, an alpine watershed, Colorado Front Range. Pages 133-137 in J. C. Halfpenny, ed. Ecological studies in the Colorado alpine: A Festschrift for John W. Marr. Inst. Arct. Alp. Res. Occ. Paper No. 37., University of Colorado, Boulder, CO.

Winget, R. N., and F. A. Mangum. 1979. Biotic condition index: Integrated biological, physical, and chemical stream parameters for management. USDA For. Serv. Intermountain Region. Contr. #40-84M8-8-524 October 17. 51 pp.

Wissmar, R. C., J. E. Richey, and D. E. Spyridakis. 1977. The importance of allochthonous particulate carbon pathways in a subalpine lake. J. Fish. Res. Bd. Can. 34:1410-1418.

Wooten, H. H. 1953. Major uses of land in the United States. USDA Technical Bulletin 1082. 253 pp.

Western Resource Development, Inc. (WRD). 1980a. Baseline vegetation inventory proposed P & J Seam Mine. Rio Blanco Co., Colo. Prepared for Northern Coal Company.

__________________. 1980b. Vegetation inventory. Snowmass coal landout facility. Garfield Co., Colo. Prepared for Gibbs and Hill, Inc., Denver, CO.

__________________. 1983. Wetland Investigations of the Adam's Rib Recreational Area, Eagle Co., Colorado. Prepared for Adam's Rib Recreational Area, Eagle, CO.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology: United States and Southern Canada. J. Wiley and Sons, New York. 501 pp.

Wright, H. E., Jr., ed. 1983. Late-Quaternary environments of the United States. Vol. I. The Late Pleistocene. S. C. Porter, ed. University of Minnesota Press, Minneapolis. 407 pp.

Wright, R. G., K. Jenkins, B. Butterfield, C. Key, and P. Happe. 1983. Wildlife habitats in riparian zones of the North Fork and mainstem Flathead River, Montana. Final Rep. Environ. Protection Agency, Helena, MT. 192 pp.

Youngblood, A. P., and W. F. Mueggler. 1981. Aspen community types on the Bridger-Teton National Forest in Western Wyoming. USDA For. Serv. Res. Pap. INT-272. Intermountain For. and Range Exp. Sta. Ogden, Utah. 34 pp.

Zoltai, S. C. et al. 1975. Developing a wetland classification for Canada. Pages 497-510 in B. Bernier and C. H. Winget, eds. Forest soils and forest land managment. Proceedings of the Fourth American Forest Soils Conference. Laval University Press, Quebec.

Zwinger, A. H., and B. E. Willard. 1972. Land above the trees. A guide to American alpine tundra. Harper and Row, New York. 463 pp.

GLOSSARY[1]

alluvial soils - deposits of sediments, clay, silt, sand, gravel, rubble, and boulders deposited by running water, ordinarily occurring on floodplains and at the base of ridges.

batholith - A great irregular mass of igneous rock with an exposed surface of more than 100 square kilometers, which has either intruded the original rock or been derived from it through metamorphism.

bog - A generalized term for a wetland that develops in a depression, such as a lake with poor drainage. Generally characterized by extensive peat deposits, acidic water, floating sedge or *Sphagnum* mats, heath shrubs, and, often, by the presence of coniferous trees. The water table is usually close to the surface without standing water (except where there are open ponds). A peat-filled or peat-covered area.

bog (ombrotrophic) - As used here, one of two main classes of herbaceous wetlands (i.e., peatlands) with organic soils. Ombrotrophic means the water source is rainwater and the bog scarcely receives more nutrients than are available in rainwater.

carr - Wetlands that occur on organic soil composed of minerotrophic peat. They have greater than 25% shrubs that may form very dense cover creating thickets, or the overstory may be open. Usually there is abundant water, which retards decomposition of peat. Willow (*Salix*) is one of the most common dominants in Rocky Mountain carrs.

cirque - The head of a glacial valley, usually amphitheatre-shaped.

deciduous angiosperm - A plant that bears flowers and seeds and drops all of its leaves seasonally.

fault - A planar or gently curved fracture in the Earth's crust across which there has been relative displacement.

fen - This is a European term applied to sedge, grass, or reed-dominated minerotrophic peatlands. The water table is at, or close to, the surface most of the time and may be acidic or basic.

forested wetland - May be located on either mixed organic or mineral substrate with a fresh water source; two kinds occur in the Rocky Mountains: coniferous and deciduous angiosperm forests.

[1]Prepared by J. T. Windell.

heath - A treeless (or nearly so) expanse of ground dominated by shrubs of the heath family (Ericaceae). A heath may or may not have peat soils.

herb wetlands - Found on either organic or mineral substrate. When on organic substrate (peatland), they are distinguished by the type of water supply and considered either minerotrophic (fen) or ombotrophic (bog). When on mineral substrate with a fresh water source they are called marsh-meadow, and when the water source is saline they are called a saline marsh-meadow.

herbaceous - A vascular plant with no persistent woody stem above ground, i.e., with the characteristics of an herb.

Histosols - Organic soils (see Soil Survey Staff, 1975).

hogback - A ridge formed by slower erosion of hard strata, but having steep, inclined slopes that are the result of either folding or faulting of the Earth's crust.

hydric soil - Soil that is wet long enough to periodically produce anaerobic conditions, thereby restricting plant life to species adapted to varying periods of saturated soils.

hydrophyte - Any plant growing in water or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content (i.e., water-logged). Refers to plants typically found in wet habitats.

hydrosere - The sum of all developmental (successional) stages from open water to well-drained forest or raised bog. Has discrete predictable steps in development that follow in clear order--hence the term succession.

kettle lake - A small hollow or depression formed when outwash was deposited around a residual block of glacial ice that later melted.

marsh - A wetland on mineral soils dominated by herbaceous (nonwoody) plants, often developing in shallow ponds or depressions, river margins, tidal areas, and estuaries. Vegetation is dominated by grasses and sedges but cattails, bullrushes, and Phragmites are often abundant. Waters are not acid.

meadow - Refers to herbaceous wetlands on mineral soil and may be synonymous with wet meadow. Meadow and wet meadow have been applied to so many types of vegetation and different ecological situations that a precise definition is not possible. Generally, meadows occur in seasonally flooded basins and flats, and soils usually are not wet during the entire growing season.

minerotrophic fen - One of the two main classes of herbaceous wetlands (i.e., peatlands). Minerotrophic means the water source has been in contact with mineral soils and provides a much greater supply of nutrients.

Montane - The ecosystem region between the Subalpine and the Grassland or High Desert ecosystem regions. Characterized by steep water-cut canyons and rolling erosional surface uplands; the terminal areas of Pleistocene glaciation usually are in the upper part of this region. Usually there are two subregions recognizable: (1) Lower Montane (or Foothill) where the vegetation is usually scrub, shrub, or open savanna type forests adjacent to the plains or desert; (2) Upper Montane, composed of a mosaic of forests and parks; dry grassland and mesic meadows, terminal and lateral moraines, and glacial lakes may occur in the Upper Montane.

peat - An accumulation of organic residues originating under more or less water-saturated conditions through the incomplete decomposition of plant and animal remains due to lack of oxygen (anaerobic), low temperatures, high acidity, or other (complex) conditions.

muck - Blackish well-decomposed peats in which the original constituents are not recognizable. Some authors require that muck contain a higher proportion of mineral sediments than peat, but this is not always true of soils that are, nevertheless called mucks. Often applied to cultivated peats. In practice, distinctions between peat and muck are unclear and it is best to simply call both organic soils.

muskeg - Said to be an Algonquin Indian word that was applied to large expanses of Sphagnum peatland. Ericaceous shrubs are typically prominent as are some trees, i.e., blackspruce and tamarack. A variety of bog. Loosely applied to any peaty area in the north or to the peat itself. Usually underlain with permafrost. Not applicable to Rocky Mountain wetlands.

ombrogenous - An adjective applied to bogs with convex surfaces and totally dependent upon precipitation for water and minerals.

organic soil - Soil composed of predominantly organic rather than mineral material. Equivalent to Histosol. Includes peats and mucks (see Soil Survey Staff, 1975).

paludification - Term used for the process of bog expansion caused by gradual raising of the water table as peat accumulation impedes drainage.

park - A term originating with early fur trappers in the Rocky Mountains and used for open grassy areas ringed with mountains. Many large intermountain basins in the Rocky Mountains bear the name "park" such as South Park, North Park, Middle Park, Colorado, but so do smaller grass-covered basins like Bergen Park and Estes Park, Colorado.

patterned fen - A fen area having alternate, more or less parallel, peat ridges and hollows oriented across the slope (i.e., at right angles to water movement). Also called strangmoor or strings and flarks.

peatland - Generic term including all classes of peat-covered terrain. Many peatlands are, in fact, a complex of bogs and fens. Equivalent to Sjor's (1950) "mire complex."

Pedalfer - A common soil type in humid regions characterized by an abundance of iron oxides and clay materials deposited in the B-horizon by leaching (Ped = soil; al = aluminum; fer = ferrous).

Pedocal - A common soil type of dry regions, characterized by accumulation of calcium carbonate in the A-horizon (ped = soil; o = of; cal = calcium).

permafrost - Permanently frozen soil, loose rock, and bed rock occurring in very cold regions where the annual heat budget is negative. May be wet or dry; ice may or may not be present.

process (ecological) - The complex interactions of organisms with other organisms and with the chemical and physical environment. Study of these dynamic processes are the core of ecological science.

raised bog - A bog with an elevated, convex central area caused by peat accumulation. The central area, at least, is isolated from the local water table and thus depends totally upon precipitation for water and minerals (i.e., ombrogenous). These are also called a highmoor or hochmoor. In Europe, raised bogs often have small ponds in the elevated section.

rhizomes - Elongate underground stems of a plant that send off shoots above and roots below. May be (and are often) tuber shaped or cordlike. Contain deposits of reserve food material.

riparian wetland - Although there is no single definition for riparian wetlands that is universally endorsed, riparian wetlands are generally considered a subset of the riparian zone. Generally includes areas that seasonally flood and may have a high water table, sometimes water-logged soils (hydric), and the presence of wetland-adapted species.

shrub - A woody plant that at maturity is usually less than 6 m (20 ft) tall and generally exhibits several erect spreading, or prostrate stems and has a bushy appearance.

shrub wetlands - Wetlands dominated with shrubs. Found on either organic or mineral substrate. When on organic substrate with a minerotrophic water source, they are considered a carr. When on organic substrate with an obmotrophic water source, they are considered a shrub bog. When on a mineral substrate with a fresh water source, they are considered a shrub wetland. When on a mineral substrate with a saline water source, they are considered a saline shrub wetland.

snowbed - A site where snow accumulates annually and stays from 7 to 10 months or more a year. These sites have a characteristic vegetation cover especially adapted to the short growing season. Snow of 2.5 feet or more maintains temperatures under the snow at around 27 °F in areas where ambient air temperatures may be as low as -65 °F.

soligenous - Adjective referring to peatlands with waters percolating through them and carrying minerals into the peatland from sources outside.

strangmoor - Uncommon in the Rocky Mountain Subalpine and Alpine, but common in the sub-Arctic. Circumboreal class of patterned bogs and fens having more or less parallel ridges (from the German "strange" or Swedish "strangar" meaning string separated by wet hollows, the Swedish "flarks" or Finnish "rimpi"). In some regions, the ridges join to form nets. Ridges lie across the slope, at right angles to water movement. The bog ridges are built of peat and support ericaceous shrubs and stunted trees. (English equivalent is string bog).

string bog - English equivalent of strangmoor.

swamp - Wetlands that have a water level above the soil surface all summer (Tansley 1939). May have tree cover of at least 25% (Zoltai 1975). By this definition, no true swamps are known to occur in the Rocky Mountains.

Subalpine - An ecological term used to denote the ecosystem below to the Alpine Zone. Ends with the treelimit ecotone between the upper limit of forest and the true tundra. Is the altitudinal counterpart, in vegetative character, to the high latitude sub-Arctic Ecosystem Region. The Subalpine is composed of a variety of community types including forests, meadows, lakes, and streams. Generally, it is in heavily glaciated terrain and often includes part (or all) of the source area of Pleistocene glaciers.

succession, primary - The ecological process by which organisms invade a bare mineral surface and change it by addition of organic materials and by physical processes. A discrete sequence of organisms and of physical and chemical changes is observable.

topogenous - Adjective indicating that the source of water for a peatland is the regional water table in a depression that predated peat formation. This indicates a "filled lake" origin.

tectonic - Movements and deformation of the Earth's crust on a large scale; caused by movements of crustal plates.

treelimit ecotone - The geographic area in which Subalpine ecosystems interfinger with Alpine ecosystems. The resulting ecosystems share characteristics of both neighboring ecosystems. Krummholz trees are a major physionomic characteristic of the treelimit ecotone, where the woody vegetation is knarled, dwarfed, and wind-pruned. Taiga is the sub-Arctic counterpart.

value (intrinsic) - A philosophically conceived worth of an object or process based upon its essential nature or constitution that is independent of human preference.

value (extrinsic) - Socioeconomic value. Objects or processes that members of a given society regard as desirable; socioeconomic beneficial consequences of an object or process.

wetland - A general catch-all term to include landscape units, such as bogs, fens, carrs, marshes, swamps, and lowlands covered with shallow and sometimes ephemeral or intermittent waters. The term also includes potholes, sloughs, wet meadows, the riparian zone, and river-overflow areas. Shallow lakes and ponds, usually with submerged and emergent vegetation as a conspicuous feature, are included in the wetland definition, but permanent waters of streams, and water deeper than 10 ft in lakes and reservoirs are not included.

APPENDIX A[1]

DOMINANT PLANT SPECIES

The most distinctive features of Rocky Mountain wetland communities are the plants that characterize and dominate them. Degree of isolation from mineral-influenced ground water controls the pattern of plant species and vegetation in Minnesota wetlands (Heinselman 1963) and may be a major factor in Rocky Mountain wetlands as well. Rocky Mountain Montane and Subalpine wetlands, however, are more variable than Minnesota wetlands, because they occur over a range of 2,591 m (8,500 ft) of elevation (from the eastern mountain front in Montana at 975 m (3,200 ft) elevation to treeline at the New Mexico-Colorado border at 3,660 m (12,000 ft), representing a variety of climate regions, and topographic and geological situations. For a more complete listing of Rocky Mountain wetland species see Reed (1986).

The following are the most abundant plant species in Rocky Mountain wetlands. Species are listed, and notes on their ecology, geographic, and altitudinal distribution are given. Plants that grow together with consistency are listed together.

Abies concolor (G.&G.) Lindl. Abundant along streamsides in southern Colorado and in Utah where mixed conifer forest borders wetlands.

Abies lasiocarpa (Hook.) Nutt. (including *Abies bifolia* and *Abies arizonica*). May be abundant along streams and in wetlands on nearly level benches, such as in *Abies lasiocarpa* - *Mertensia ciliata* habitat type (DeVelice et al. 1984).

Acer grandidentatum Nutt. Common along some stream courses in Utah.

Acer negundo L. An abundant tree along stream courses at mid to low elevations throughout the Rocky Mountains.

Alnus oblongifolia Torr. A characteristic tree along stream courses in southern New Mexico.

Alnus tenuifolias Nutt. A characteristic tall shrub along rivers and streams throughout the Rocky Mountains.

Betula fontinalis Sarg. (*B. occidentalis*). An abundant tall shrub along Montane and lower Subalpine streams and rivers in the Rocky Mountains.

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[1]Prepared by D. J. Cooper.

Betula glandulosa Michx. Abundant throughout Subalpine Rocky Mountain wetlands and an indicator of wet, little humified peat (Phillips 1977). Common on Sphagnum hummocks in bogs in Colorado in the Cross Creek region, Sawatch Range, at iron-rich springs near Crested Butte, on successional wetlands of Subalpine glacial lakes, and in the Colorado River Valley of Rocky Mountain National Park. Widely distributed throughout the Rocky Mountains.

Calamagrostis canadensis (Michx.) P. Beauv. Can be an indicator of old beaver ponds, where it dominates communities in Rocky Mountain National Park (Wilson 1969). This taxon dominates stands with higher standing water table than Carex utriculata and C. aquatilis. Communities dominated by it also occur in the Indian Peaks area (Komarkova 1979) and in glaciated valleys on the eastern side of Rocky Mountain National Park (Willard and Marr 1960, 1961). It is common throughout the Rocky Mountain system. Calamagrostis inexpansa is also dominant in some situations.

Caltha leptosepala DC. Dominates vegetation of springs and seeps in the Colorado Front Range in Rocky Mountain National Park (Wilson 1969), in the Indian Peaks region (Komarkova 1979), and on Utah's Wasatch Plateau (Ellison 1954). This taxon is common in Subalpine and Alpine wetlands throughout the Rocky Mountains. It may be replaced by Caltha biflora in western Montana and Idaho (Steele et al. 1983). Often with Trollius larus in the Subalpine Zone.

Carex aquatilis Wahlenb. In Rocky Mountain National Park, Colorado this species occurs where soils are less flooded than where C. utriculata occurs. It is found where water depth is from 25 cm above the soil surface to a water table 30 cm below the soil surface (Wilson 1969). C. aquatilis spp. stans occurs in the Subalpine and low Alpine Zones, whereas C. aquatilis spp. aquatilis occurs in the Montane zone (Wilson 1969) of this same area. Vegetation dominated by this taxon is reported for the Indian Peaks area and Big Meadow in the Colorado Front Range (Bierly 1972; Komarkova 1979) and is common throughout the Rocky Mountains. This taxon occupies the coolest soil sites (19 °C, average July temperature) found in the Colorado Subalpine Zone and soil nutrients are more important than temperature in determining plant size (Chapin 1981).

Carex utriculata Boott. Occurs in the wettest and most persistently flooded habitats in Rocky Mountain National Park, Colorado, and is more abundant in the Montane than Subalpine Zone (Wilson 1969). It is one of the most abundant wetland species in the Cross Creek wetlands of the Sawatch Range (Cooper 1986) and dominates vegetation at the inlet to Grand Lake, Colorado (Johnson 1941). This taxon dominates stands where approximately 3 dm of water occur in June. It provides 79.5% of the vegetative cover and has the lowest species diversity of any vegetation type in the Big Hole National Battlefield, Montana (Pierce 1982).

Carex spp. Numerous species of Carex dominate Rocky Mountain wetland ecosystems including C. nebraskensis, C. simulata, C. lasiocarpa, C. siccata, C. nigricnas, C. festivella, C. microptera, C. limosa, C. pachystachya, C. scopulorum, C. scoparia, C. pyrenaica, C. praegracilis, C. vesicaria, and others.

Corylus cornuta Marsh. A dominant of some canyon bottoms along the eastern Rocky Mountain front.

Deschampsia caespitosa (L.) P. Beauv. Communities dominated by D. caespitosa occupy deep snowbeds in the Upper Subalpine and Alpine Zones (Marr 1967; Bierly 1972; Schlatterer 1972; Komarkova 1979; Willard 1979). Mueggler and Stewart (1980) reported that in Montana this taxon dominates the Deschampsia - Carex habitat type, which occurs in areas flooded by snowmelt in late spring and early summer, at 6,000 to 9,000 feet elevation. This community type is the most productive grassland type in western Montana, with 2,906 kg/ha dry matter, of which 26% may be Deschampsia and 56% Carex spp. This vegetation type also has the greatest species diversity at the Big Hole Battlefield, Montana, with 30 species (Pierce 1982). Deschampsia is a circumpolar and bipolar taxon and is common in a variety of snow-covered habitats, but it is not abundant in the standard fen gradient from Carex utriculata to Calamagrostis canadensis. It does show up sporadically, however, in bogs with Sphagnum spp., and may be the most abundant graminoid in flood-irrigated wetlands in Colorado's mountain parks, e.g., Middle Park.

Distichlis spicata (L.) Greene var stricta (Torr.) Beetle. Abundant on alkaline soils.

Eleocharis acicularis (L.) R.&S. A dominant and aggressive colonizer of wet mud, such as on meander point bar deposits in Boulder Park, Colorado (Vestal 1914). Widely distributed across the Rocky Mountains, from the plains to alpine.

Eleocharis macrostachya Britton. Occurs as an emergent in many ponds, but also in temporary ponds, some of which may be alkaline.

Eleocharis palustris (L.) R.&.S. Occurs on warmer soils than Eriophorum angustifolium or Carex aquatilis in Colorado.

Eleocharis pauciflora (Lightf.) Link (E. quinqueflora). Dominates vegetation on the deepest peat, 40 to 125 cm, found in Rocky Mountain National Park, Colorado (Wilson 1969). It occurs where there is shallow flooding all summer and deeper flooding than sites where Caltha leptosepala occurs on Utah's Wasatch Plateau (Ellison 1954).

Epilobium latifolium L. and Mimulus guttatus DC. Characteristic of gravelly alluvium along streams throughout the Subalpine Zone of the Rocky Mountains.

Equisetum arvense L. Abundant at springs and seeps in the Montane and Subalpine Zones throughout the Rocky Mountains.

Erigeron peregrinus. Can dominate vegetation where the water table is more than 15 cm below the soil surface, but is never dry (Wilson 1969). It occurs throughout the Rocky Mountains.

Glyceria borealis (Nash) Batch. Abundant in flood-irrigated wetlands in Colorado's San Luis Valley, and common throughout the Rocky Mountains.

Hippuris vulgaris L. Abundant in shallow ponds in the Montane Zone throughout the Rocky Mountains.

Juncus arcticus Willd. (J. balticus). Vegetation dominated by this taxon is common throughout the Montane Zone of the Rocky Mountains. Pierce (1982) reports that this taxon is an increaser in overgrazed rangeland and communities dominated by it probably did not exist prior to the mid-1880's.

Juncus spp. Other species of Juncus dominate wetlands in the Subalpine Zone of the Rocky Mountains, including J. mertensianus, J. parryi, and J. castaneus.

Nuphar luteum Subth. & Sm. ssp. polysepalum (Engelm.) Beal. Abundant in ponds in the Montane and Subalpine Zones throughout the Rocky Mountains.

Pentaphylloides floribunda (Pursh) A. Love. (Potentilla fruticosa). Dominates drier stands on the edges of wetlands such as pond seres throughout the Rocky Mountains.

Picea engelmannii (Parry) Engelm. May be abundant in wetland types such as the Abies lasiocarpa - Mertensia ciliata and P. engelmannii - Heraculum spondylium habitat types in Colorado (DeVelice et al. 1984). Generally widespread dominant of forests in the Subalpine Zone throughout the Rocky Mountains.

Picea pungens Engelm. Abundant and endemic to southern and central Rocky Mountains, where it occurs along many streams and rivers in the Montane Zone.

Populus X acuminata Rydb. An abundant tree along stream courses in the lower eastern foothills of the Colorado Front Range (Marr 1967).

Populus angustifolia James. The most abundant deciduous tree along streams, rivers, and some lakes in the Rocky Mountains.

Populus tremuloides Michx. May dominate some wetlands throughout the Rocky Mountains.

Salix drummondiana Barratt ex. Hook. In mesic to dry environments in Colorado's Laramie River Valley (Phillips 1977) and elsewhere throughout the Rocky Mountains.

Salix exigua Nutt. Many times the most abundant willow in canyons and other low-elevation mountain areas throughout the Rocky Mountains.

Salix geyeriana Anderss. and S. monticola Bebb. Both dominate the driest portion of wetland environments (Phillips 1977). Their abundance increases with increasing distance away from streams in North Park, Colorado (Cannon and Knopf 1984). Both occur throughout the Rocky Mountains.

Salix phylicifolia L. ssp. planifolia (Pursh) Hiitonen, S. brachycarpa Nutt., S. glauca L. These willows are the most abundant shrubs in the Subalpine Zone, above 9,200 feet elevation in Colorado. S. planifolia may be dominant as low as 9,000 feet in Cross Creek in the Sawatch Range of Colorado (Cooper 1986). These taxa dominate communities in the Indian Peaks region (Komarkova 1979) and on the western slope of Rocky Mountain National Park in the Colorado Front Range (Bierly 1972). The percentage of S. planifolia decreases with increasing distance from streams in Colorado's North Park

(Cannon and Knopf 1984), and it is found on soils with high humification along the Laramie River (Phillips 1977). Vegetation dominated by S. planifolia occurs along streams, as well as where there is shallow snow accumulation, and in shallow basins produced by solifluction. It is replaced by Carex aquatilis where soil is more saturated, and by Deschampsia caespitosa where snow persists longer (Heifner 1974).

Salix wolfii Bebb. Indicates wet, low-humified peat in Colorado's Laramie River Valley (Phillips 1977). Widely distributed throughout the Rocky Mountains.

Salix spp. Other species of Salix that can dominate wetlands in the Rocky Mountains include S. caudata, S. bebbiana, S. irrorata, S. lasiandra, S. lutea, S. pseudocordata, S. lasiolepis, S. goodingii, S. barrattiana, S. eastwoodiae, S. commutata, S. candida, and others.

Sarcobatus vermiculatus (Hook.) Torrey. Dominant over large areas on alkaline soils with high water table, most notably in Colorado's San Luis valley, but throughout the Rocky Mountains.

Senecio triangularis Hook. A dominant species along streams, springs, and ponds in the Subalpine and Montane. Typically found with S. serra, Mertensia ciliata, Heraculum lanatum, Cardamine cordifolia, Trollius laxus, Delphinium barbeyi, Saxifraga odontoloma, Aconitum columbianum, Castilleja rhexifolia, Juncus mertensianus, Pedicularis groenlandica, and Primula parryi. In addition, the following taxa dominate vegetation in the Lower Alpine Zone and Subalpine Zone of the Indian Peaks region of Colorado (Komarkova 1979): Athyrium distentifolium, Carex illota, Carex vernacula, and Eleocharis quinquenervis. Delphinium barbeyi is dominant in wetlands on Utah's Wasatch Plateau, where it surely has increased due to heavy sheep grazing of taxa such as Heraculum lanatum, Polemonium foliolosum, Osmorrhiza occidentalis, Valeriana occidentalis, Mertensia leonardi, Agropyron trachycaulon, Angelica pinnata, Erigeron speciosus, Bromus carinatus, B. anomala, Carex festivella, C. hoodii, C. raynoldsii, Aquilegia caerulea, and Castilleja sulphurea which composed the pristine mixed upland herb association on Utah's Uinta Mountains, yet are all now uncommon.

Sporobolus airoides (Torr.) Torr. Abundant on alkaline soils.

Sparganium angustifolium Michx. Dominates shallow ponds with standing water from several inches to two feet in depth (Vestal 1914; Cooper 1986).

Typha latifolia L. and T. angustifolia L. Abundant in roadside ditches and shallow ponds in Montane, throughout the Rocky Mountains.

APPENDIX B[1]

CHARACTERISTIC ANIMALS OF ROCKY MOUNTAIN WETLANDS

VERTEBRATA

MAMMALS[a]

Moose (Alces americana) B
Mule deer (Odocoileus hemionus) U
Whitetail deer (Odocoileus virginianus) U
Pronghorn (Antilocapra americana) X
Elk (Cervus canadensis) U
Bighorn sheep (Ovis canadensis) M
Beaver (Castor canadensis) B
Muskrat (Ondatra zibethica) B
Coyote (Canis latrans) M
Mountain lion (Felis concolor) M
Bobcat (Lynx rufus) M
Red fox (Vulpes fulva) U, M
Kit fox (Vulpes velox) U, M
Gray fox (Urocyon cinereoargenteus) U, M
Black bear (Ursus americanus) U, M
Grizzly bear (Ursus horribilus) U, M
Wolverine (Gulo luscus) M
Pine marten (Martes americana) M
River otter (Lutra canadensis) B
Mink (Mustela vison) U
Longtail weasel (Mustela frenata) U
Least weasel (Mustela rixosa) U
Striped skunk (Mephitis mephitis) U
Spotted skunk (Spilogale putorius) U
Badger (Taxidea taxus) X
Snowshoe hare (Lepus americanus) U
Mountain cottontail (Sylvilagus nuttalli) U
Desert cottontail (Sylvilagus auduboni) U
Pigmy rabbit (Sylvilagus idahoensis) U
Ground squirrels (Citellus spp.) X
Raccoon (Procyon lotor) X
Northern pocket gopher (Thomomys talpoides) U
Valley pocket gopher (Thomomys bottae) U
Field mice (Peromyscus spp.) U

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[1]Prepared by S. Q. Foster and B. E. Willard.

VERTEBRATA (Continued)

MAMMALS (Concluded)

Meadow vole (Microtus pennsylvanicus) B
Mountain vole (Microtus montanus) B
Mountain redbacked vole (Phenscomys intermedius) B
Masked shrew (Sorex cinereus) B
Northern water shrew (Sorex palustris) B
Vagrant shrew (Sorex vagrans) B

BIRDS[b]

Pied-billed grebe (Podilymbus podiceps) B
Horned grebe (Podiceps auritus) M
Eared grebe (Podiceps nigricollis) B, M
Western grebe (Aechmophorus occidentalis) B, M
Red-necked grebe (Podiceps grisegena) B
Common loon (Gavia immer) M
Double-crested cormorant (Phalacrocorax auritus) B, M
Great blue heron (Ardea herodias) B
Snowy egret (Egretta thula) B, M
Black-crowned night heron (Nycticorax nycticorax) B
Canada goose (Branta canadensis) B, M
Green-winged teal (Anas crecca) B
Blue-winged teal (Anas discors) B, M
Cinnamon teal (Anas cyanoptera) B
Mallard (Anas platyrhycos) B
Northern pintail (Anas acuta) B, M, W
Northern shoveler (Anas clypeata) B, M
Gadwall (Anas strepera) B, M
American wigeon (Anas americana) B, M
Canvasback (Aythya valisineria) B, M
Redhead (Aythya americana) B, M
Ring-necked duck (Aythya collaris) B, M
Lesser scaup (Aythya affinis) B, M
Common goldeneye (Bucephala clangula) W, M
Barrow's goldeneye (Glaucionetta islandica) M
Bufflehead (Bucephala albeola) W, M
Common merganser (Mergus merganser) B
Red-breasted merganser (Mergus serrator) W, M
Ruddy duck (Oxyura jamaicensis) B, M
Bald eagle (Haliaeetus leucocephalus) b, W, U, #
Virginia rail (Rallus limicola) B
Sora rail (Porzana carolina) B
American coot (Fulica americana) B
Sandhill crane (Grus canadensis) B, M
Whooping crane (Grus americana) M, #
American avocet (Recurvirostra americana) B, M

VERTEBRATA (Continued)

BIRDS (Concluded)

Solitary sandpiper (Tringa solitaria) M
Willet (Catoptrophorus semipalmatus) B, M
Spotted sandpiper (Actitis macularia) B
Least sandpiper (Calidris minutilla) M
Baird's sandpiper (Calidris bairdii) M
Wilson's phalarope (Phalaropus tricolor) B, M
Franklin's gull (Larus pipixcan) M
Ring-billed gull (Larus delawarensis) M
Trumpeter swan (Cygnus buccinator) M,#
Whistling swan (Cygnus columbianus) U, M, W
Western kingbird (Tyrannus verticalis) B
Violet-green swallow (Tachycineta thalassina) B
American dipper (Cinclus mexicanus) B
Yellow warbler (Dendroica petechia) B
Yellow-rumped warbler (Dendroica coronata) B
Common yellowthroat (Geothlypis trichas) B, M
Wilson's warbler (Wilsonia pusilla) B
Song sparrow (Melospiza melodia) B
White-crowned sparrow (Zonotrichia leucophrys) B
Red-winged blackbird (Agelaius phoeniceus) B
Yellow-headed blackbird (Xanthocephalus xanthocephalus) B

REPTILES[c]

Common snapping turtle (Chelydra serpentina serpentina) B
Western painted turtle (Chrysemys picta belli) B
Ornate box turtle (Terrapene ornata ornata) B
Western spiny softshell (Trionyx spiniferus hartwegi) B, #
Red-lipped prairie lizard (Sceloporus undulatus erythrocheilus) B
Prairie-lined racerunner (Cnemidophorus sexlineatus viridis) B
Plateau striped whiptail (Cnemidophorus velox) B
Variable skink (Eumeces multivirgatus gaigeae) B
Great Plains skink (Eumeces obsoletus) B, #
Eastern yellowbelly racer (Coluber constrictor flaviventris) B
Great Plains rat snake (Elaphe guttata emoryi) b
Plains hognose snake (Heterodon nasicus nasicus) B
Milk snake (Lamprepeltis triangulum) B
Desert striped whipsnake (Masticophis taeniatus taeniatus) B
Northern water snake (Nerodia sipedon sipedon) B
Western smooth green snake (Opheodrys vernalis blanchardi) B
Great Basin gopher snake (Pituophis melanoleucus deserticola) B
Bullsnake (Pituophis melanoleucus sayi) B
Gopher snake (Pituophis melanoleucus ssp.) B
Plains blackhead snake (Tantilla nigriceps nigriceps) B
Wandering garter snake (Thamnophis elegans vagrans) B
Red-sided garter snake (Thamnophis sirtalis parietalis) B
Northern lined snake (Tropidoclonion lineatum lineatum) B

VERTEBRATA (Concluded)

AMPHIBIANS[c]

Tiger salamander (*Ambystoma tigrinium*)[d] B
Boreal toad (*Bufo boreas boreas*) B
Great Plains toad (*Bufo cognatus*) B
Woodhouse's toad (*Bufo woodhousei woodhousei*) B
Boreal chorus frog (*Pseudacris triseriata maculata*) B
Bullfrog (*Rana catesbiana*) B
Northern leopard frog (*Rana pipiens*) B
Wood frog (*Rana sylvatica*) B, #
Plains spadefoot (*Scaphiopus bombifrons*) B
New Mexico spadefoot (*Scaphiopus multiplicatus*) B

FISHES

White sucker (*Catostomus commersoni*)
Flannelmouth sucker (*Catostomus latipinnis*)
Western longnose sucker (*Catostomus catostomus*)
Bluehead sucker (*Catostomus discobolus*)
Mountain sucker (*Catostomus platyrhynchus*)
Rio Grande sucker (*Catostomus plebius*)
Longnose dace (*Rhinichthys cataractae*)
Colorado speckled dace (*Rhinichthys osculus*)
Creek chub (*Semotilus atromaculatus*)
Fathead minnow (*Pimephales promelas*)
Red shiner (*Notropis lutrensis*)
Sand shiner (*Notropis stramineus*)
Piute sculpin (*Cottus beldingi*)
Mottled sculpin (*cottus bairdi*)
Mountain whitefish (*Prosopium williamsoni*)
Golden trout (*Salmo aquabonita*)
Rio Grande cutthroat (*Salmo clarki virginalis*)
Colorado cutthroat (*Salmo clarki pleuriticus*)
Greenback cutthroat (*Salmo clarki stomias*)
Snake River cutthroat (*Salmo clarki*)
Yellowstone cutthroat (*Salmo clarki lewisi*)
Rainbow trout (*Salmo gairdneri*)
Brown trout (*Salmo trutta*)
Brook (trout) char (*Salvelinus fontinalis*)
Arctic grayling (*Thymallus arcticus*)

INVERTEBRATA[e]

MOLLUSCA

Gastropoda fresh water limpets, snails X

Pelecypoda--Large unionid clams do not occur in mountainous areas chiefly because of the absence of the proper fish species, which serve as hosts for the (immature) glochidial stages of the clams. Seed clams (Sphaeriidae), however, are common in springbrooks and small lakes at elevations up to 10,000 feet in mud, sand, and gravel substrates. They feed on finely divided suspended organic matter and presumably are not related to wetlands problems.

ARTHROPODA

INSECTA (Orders)

Aquatic insects are undoubtedly the group most closely related to wetlands phenomena, chiefly because of their dependence upon marginal shrubs, trees, grasses, and emergent hydrophytes as physical objects for perching, resting, and mating activities of the aerial adult stages. We find here the major orders of aquatic insects.

Plecoptera (stoneflies) X all immature need wet areas to complete life cycle
Ephemeroptera (mayflies) X ditto
Odonata (damsel/dragonflies) X ditto
Hemiptera (true bugs) X some are found in wetlands
Megaloptera (alderflies, some are dobsonflies, troutflies) X
Tricoptera (caddisflies) X all have aquatic larvae
Diptera (flies, mosquitos, midges) some need water to complete life cycle
Coleoptera (beetles) some are found in wetlands; some are aquatic

While the immatures (larvae and nymphs) are restricted to aquatic habitats, the adults emerge and mate along lakeside or streamside. Here most species must have growths of marginal vegetation, especially shrubbery. If grazing activities and traffic by stock animals keep the vegetation browsed down to a thin growth of grasses, then obviously the mating activities of emerged insects will be severely reduced, and the stream or pond will have reduced populations.

Collembola (springtails) X
Lepidoptera (butterflies/moths) a few have aquatic caterpillars

INVERTEBRATA (Continued)

ARACHNIDA (Order)

Hydracarina (water mites)

CRUSTACEA (Orders) All are aquatic

Anostraca (fairy shrimp) Notostraca (tadpole shrimp) and Conchostraca (clam shrimp) are typical of temporary pools and ponds in the high country. They never occur in waters where fish are present, and the temporary nature of their habitat is essential to their life cycle.

Cladocera (water fleas, Daphnia) X chiefly in fresh water
Eucopepoda (Copopods) X chiefly in fresh water
Podocopa (seed shrimp)
Mysidacea (Opossum shrimp) X three fresh water species

Isopoda and Amphipoda (scuds, side swimmers, and aquatic sowbugs) are largely organic detritus feeders and in this sense are dependent upon allochthonous organic matter in small lakes and weedy ponds. Rarely are they found in sluggish sections of mountain streams. Destruction of pond - and lakeside vegetation undoubtedly affects the density of these two taxa.

Decapoda (crayfish). As recently as 130 years ago, crayfish were almost unknown above altitudes of 6,500 feet in the Rocky Mountain area. More recently, however, they have been accidentally and intentionally planted in ponds, lakes, reservoirs, and sluggish streams; consequently collection records between 6,500 and 8,500 feet are increasing. Undoubtedly crayfish populations will steadily increase and spread during the years to come. They do best in the shallows where there are growths of hydrophytes to serve as a food source.

ANNELIDA

Macroannelids, including leeches, are found along the margins of streams and rivers in the damp soil--one of the few places where earthworms are found in mountainous areas. they sometimes stray into the stream proper where they are consumed by fish. Loss of marginal vegetation probably decreases earthworm densities. In general, earthworms are uncommon in our mountains because of the low calcium content of the soils. Leeches, however, are abundant in ponds and small lakes; a few small species may be found in streams. Because they are vagile, leeches have no problem in adjusting to varying water levels. A few species are vegetarians and feed on marginal hydrophytes.

Groups occurring in the Rocky Mountains are Oligochaetes (aquatic earthworms), Branchiobdellida, Polychaeta, and Hirudinea (leeches).

INVERTEBRATES (Concluded)

BRYOZOA (ECTOPROCTA) (Moss animalcules)

This group of sessile species cannot stand exposure to air, even though they prefer the shallows of slow but clear streams, lakes, and ponds, where they attach to twigs, stems, roots, and rocks. A temporarily lowered water level will extirpate populations, although their resting stages will produce new, massive colonies at a later date when water levels are restored.

TARDIGRADA (Water bears)

NEMATOMORPHA (Horsehair worms)

ROTATORIA (Rotifers)

GASTROTRICHA

NEMERTEA (Proboscus worms)

PLATYHELMINTHES--flatworms

Macroturbellarians, such as Planaria and its relatives are seldom associated with marginal wetlands, but are typical of pebble and stony substrates in streams and springbrooks. Watercress is also a preferred substrate.

CNIDARIA (COELENTERATA)

Hydra--The genus Hydra and its relatives are typically found in shallow ponds, especially when they can attach to permanently submerged grasses, hydrophytes, or submerged basal portions of pond-side shrubs (e.g., willows). They are rare in mountain streams.

Some colonial polyps and one species of fresh water jellyfish are found in the Rocky Mountains.

PORIFERA--fresh water sponges

This group seldom lives in running waters unless the current is sluggish and the water is free of suspended solids. More typically, they can be found on the near-shore bottom attached to stones, twigs, and branches. Changes in water level that expose sponges to air, however briefly, are fatal, since they are not motile. In mountainous areas, freshwater sponges are most common in small lakes, ponds, and beaver ponds.

PROTOZOA--

Are primarily aquatic; some species are found in soils and in decaying organic matter of wetlands.

Footnotes

[a]Common mammals of Rocky Mountain wetlands according to Burt and Grossenheider 1952.

[b]Common birds in wetlands of the Colorado Rocky Mountains according to Chase, et al. (1982), comparable lists exist in other States.

[c]Common reptiles and amphibians in wetlands of the Colorado Rocky Mountains according to Hammerson and Langlois 1981; comparable lists exist in other States.

[d]One group of populations in the Elk Mountains of Colorado has evolved in concert with a series of ponds with specific unusual characters (Sexton and Bizer 1978).

[e]Invertebrates taken from Pennak, R. W. 1978. Comments by Dr. Robert W. Pennak, Professor Emeritus of Aquatic Biology, University of Colorado at Boulder, Department of Environmental, Population, and Organismic Biology.

Rare
B--definite breeder b--likely breeder M--migrates through W--winter visitor
X--present in some types of wetlands
U--uses wetlands for rest and/or feeding
RR--riverine and lake species

APPENDIX C[1]

ECONOMIC THEORY AS IT RELATES TO WETLAND VALUES

Economic value involves consideration of what is most efficient and equitable. Efficiency is evaluated through the technical exercise of benefit/cost analysis (BCA), which determines whether some aspect or all of society becomes wealthier either as the result of a proposed change in a natural resource allocation or without the proposed change. BCA can be very useful in providing information to decisionmakers, however, it is the public laws and politics, not BCA, that determine whether costs and benefits are fairly distributed or equitable (Peterson 1985).

Before undertaking a BCA, it is important to clearly define what is being valuated. Economists are concerned with whether the aggregate wealth or quality of life is increased before or after (with or without) an action on a natural resource (Peterson 1985). For example, a BCA could be performed to determine whether the value of a wetland is greater in its preserved natural state or with a golf course covering 50% of its surface area.

A second important consideration is to identify the accounting stance of the study. There is a great deal of controversy here, because different people involved have different objectives. Will economic growth or increased wealth accrue to the welfare of society in general (the public trust stance)? Is it to improve the economic health of the government (the balanced budget stance)? Or is it to promote growth in capital or income in the private sector (the private profit stance)? The public trust stance is concerned more with the National well-being than with the wealth of government or private individuals or corporations (Peterson 1985).

BCA is often based upon financial interactions in which money actually changes hands. It also recognizes "consumer surplus" or net willingness of individuals to pay for a good or opportunity over and beyond existing expenses and before going without the opportunity (Sorg and Loomis 1984). Economic efficiency is reached when the sum of benefits due to a proposed action (or nonaction) is greater than the sum of the losses due to the alternative(s), regardless of the identity of the winners or losers. When there are competing options (i.e., preservation, golf course, gravel mining, road construction), the most efficient route will be the one with the greatest aggregate gains (Rosenthal et al. 1984).

The trusthworthiness of the economic estimate by BCA is only as accurate as the data that go into it. At present, in the case of Rocky Mountain

[1]Prepared by S. Q. Foster.

wetlands, the empirical data on natural functions and flow of services is limited and difficult to quantify. It is even harder to predict impacts resulting from a proposed action. BCA is criticized because it may give a false impression of precision, when the data base on natural systems is not strong. The willingness-to-pay method of determining consumer surplus is not an appropriate means for valuating natural resources when the user does not know enough to make wise value estimates (Peterson and Randall 1984).

The total value of wetlands stems from on-site and off-site uses (Figure 1). On-site use may result in consumption of goods (i.e., elk-hunting, trapping, mining) or nonconsumptive activities (i.e., hiking, swimming, river-running). A portion of on-site activities have financial value, when cash changes hands during permitting, boat rentals, camp-site fees, or the like. Off-site wetland uses include option, existence, and bequest values. Money is not exchanged over them, but they are of economic value in the sense that the citizen may be willing to pay for the preservation of any or all of them. Option value refers to the user's willingness to pay to preserve a wetland recreational opportunity that may be threatened by some change in policy. Existence value applies to the willingness of individuals to pay for the continued existence of the wetland, just to know that it exists. Bequest value is the willingness to pay for the opportunity of future generations to have access to wetland resources and amenities (Loomis et al. 1985).

Three methods are commonly used to determine empirical economic value of wild resources: (1) Gross Expenditure Method, (2) Travel Cost Method, and (3) Contingent Value Method.

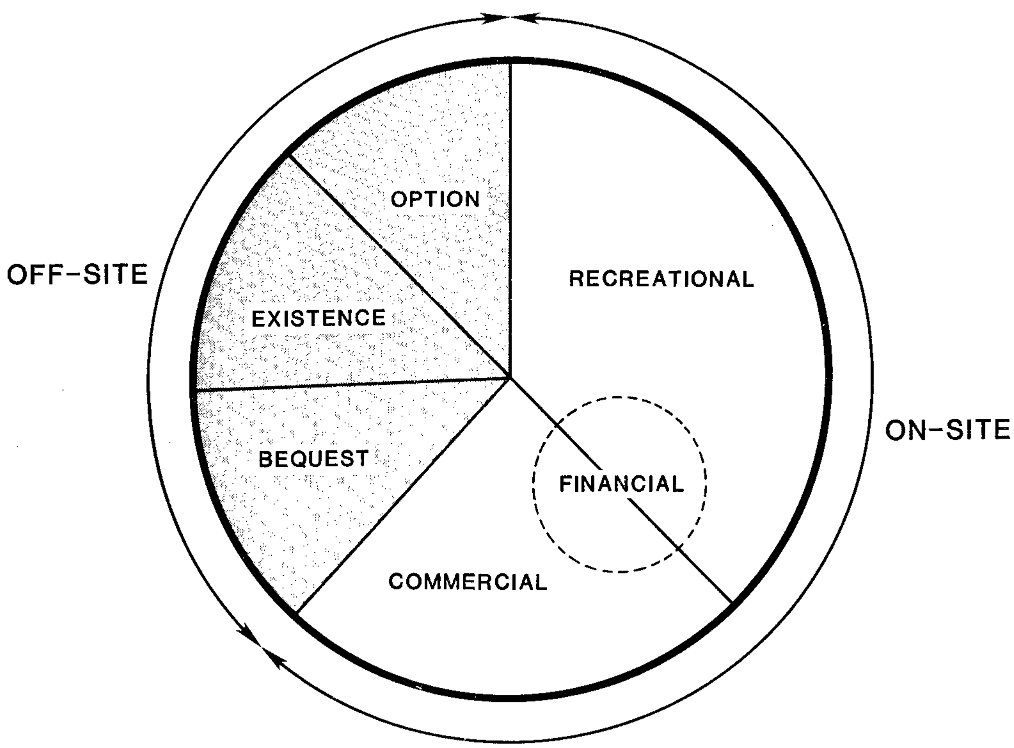

Figure 1. Total value of wetlands includes on-site (recreational and commercial) and off-site (option, existence, and bequest) values. (From Peterson 1985.)

The Gross Expenditure Method (GEM) assumes that the value of an activity equals the total amount of money spent doing it (Sorg and Loomis 1984, 1985). For example, the value of birdwatching in a wetland is represented by total expenses of the bird watcher in travel costs, food, lodging, and equipment related to that wetland activity. GEM has been used extensively because: (1) data are fairly easy to obtain; and (2) it is a good indication of the effects of the sport on local economy. GEM has some serious drawbacks as a measure of economic efficiency for resource allocation. For example, a wetland manager wishes to know if addition of birdwatching blinds is an economically feasible site improvement. It is necessary for the management costs of the improvement to be compared with potential benefits. GEM alone will not meet management needs, because it fails to provide information on net benefits. It is this net value in excess of costs that measures real monetary value lost if additional bird watching opportunities are not made available (Sorg and Loomis 1984). A second limitation of GEM is that it is biased against wildlife and off-site uses of natural areas, since they are not readily assessed monetary value (Sorg and Loomis 1985).

Travel Cost Method (TCM) is a tool for determining empirical benefits from uses of recreational areas. TCM utilizes travel costs to the sites as a proxy for price. Travel costs are assumed to represent the user's willingness to pay for use of a site over and above existing costs (Rosenthal et al. 1984). The method may be useful to: (1) determine net economic value of a recreation site, (2) determine net economic value of a proposed modification to this site or an entirely new site, (3) allocate funds more efficiently among programs, (4) predict users' travel behavior, and (5) predict changes in site use resulting from changes in fees for that site utilization. TCM is particularly useful when trips are made with the sole purpose of visiting the site in question. Difficulties arise in its application when trips include other purposes and value of time spent traveling are recognized (Sorg and Loomis 1984, 1985). From the management perspective, TCM falls short in distinguishing what portion of the user's satisfaction on a visit was due to natural assets (i.e., birds, vegetation, scenery) versus some management characteristic of the site (i.e., campsite facilities, interpretive walks, reservation system).

The Contingent Value Method (CVM) is also called the "bidding game." Resource users are presented with a questionnaire in personal interviews, by telephone, or by mail. They are asked to determine their own consumer surplus by suggesting hypothetical prices they would be willing to pay in order to preserve a given opportunity, or to experience an alternative opportunity resulting from a change in the status of the area used (Sorg and Loomis 1985). A maximum willingness-to-pay is reached by asking the user if he or she would pay certain amounts, incrementally increased, until an upper limit is reached. The success of CVM is dependent upon the quality of the questionnaire, which must be well-defined and free of bias.

Both TCM and CVM are appropriate tools for determining consumer surplus with regard to marketable and nonmarketable resources. They are also useful in estimating positive and negative impacts on wildlife resulting from a management direction. Means are available to allow comparisons across the studies using the two different methods (Sorg and Loomis 1985).

It is important to remember, however, that benefit/cost analysis involves questions of efficiency and equity. Efficiency is based upon consumers' willingness-to-pay as measured by either marketplace transactions (GEM) or some indirect measure (TCM or CVM). Equity questions arise when uneven distribution of income in a canvassed group affects willingness to pay estimates or when a proposed management plan has potential for economic impact on employment or income in some sector of the immediate geographic area. Issues of equity are essentially political in nature and must be recognized and solved in that forum.

APPENDIX D[1]

RESEARCH NEEDS

A wide variety of investigations about Rocky Mountain wetlands are needed before we will have a comprehensive understanding of wetland types, functions, values, and of the effects of impacts on wetlands. The following are research needs identified by the various authors of this document; these needs are not prioritized.

Types and Structures of Wetlands

- Make a regional study of Rocky Mountain wetlands, covering plants, animals, soils, bedrock, hydrology, water quality, distribution of community types, and their condition.

- Establish baseline reference areas for creating a permanent data base and time line on Rocky Mountain wetland vegetation, soils, animals, hydrology, and the ecological interactions of these factors.

- How fast does succession take place in the different types of wetlands?

- How long does soil need to be saturated to support a different array of wetland plants and a different plant community?

- Do true ombrogonous bogs occur in the Rocky Mountains? If not, why not? If so, what local conditions allow them to develop?

- How do various bedrock types (limestone, granite, etc.) affect the type of wetland that develops, and its floristic composition and productivity?

- What are the relationships between the hydrologic regime of streams and the pattern of the stream? At what rate does this pattern form?

- What is the status of the habitat for populations of threatened and endangered species of animals and plants associated with wetlands in the Rocky Mountains?

- How does species composition vary with elevation and latitude in Rocky Mountain wetlands? How is this variation related to differences in function and to differences in geography and history of the site?

- Describe the hydrological regime of various major types of Rocky Mountain wetlands.

[1]Prepared by all authors.

Wetland Functions

- How do wetland functions vary with elevation and latitude in the Rocky Mountains?

- What are the effects of wetland functions on local, regional, and global climatological and meteorological phenomena? What are the consequences of wetland disturbance or destruction on these phenomena?

- Identify the hydrological processes associated with various types of Rocky Mountain wetlands. What wetland types (if any) are involved with aquifer discharge and with recharge?

- How much tolerance do plant species have for changes in, and duration of changes, hydrological regime? How is this influenced by season in which flooding occurs? What changes in species composition occur with changes in hydrological regime?

- What is the amount of primary production in the various types of Rocky Mountain wetlands? How does primary production compare with that in upland ecosystems and with other wetlands?

- How does nutrient cycling vary among the different types of Rocky Mountain wetlands?

- What load of contaminants can wetlands store without impairment of natural functions? How long do they retain toxic pollutants before they decompose? What is their acid precipitation buffering capacity?

Values of Wetlands

- What are the roles of various types of wetlands in flood control?

- What are the roles of Rocky Mountain wetlands in nutrient cycling, soil stabilization, water purification, and toxic substance trapping?

- What is the role of various wetland types in contributing organic matter to detritus-based food chains in adjacent waterways?

- Continue to elucidate the roles of wetlands in supporting wildlife and invertebrates. Develop lists of plants and animals that are dependent on wetlands for habitat, breeding places, or food.

- Continue to identify those wetlands worthy of preservation, based on their unique or essential functions, or on their being the habitat for threatened and endangered species that reside, breed, or feed in them.

- Develop programs to educate the public about the nature and importance of wetlands.

- Investigate the effects of human recreational uses on Rocky Mountain wetlands. How are different wetland types used? With what frequency and intensity? What wetland types are used most?

- Within valuation methodology, develop a means for predicting irreversible trends resulting from wetland destruction that can be used in decision-making and policy formulation.

- Develop methods and predictive models for determining the values of artificially created wetlands--those created to mitigate wetland destruction elsewhere.

Economics of Wetlands

- Investigate the possibility of establishing a standardized list of social benefits from wetlands in the Rocky Mountain region. Analyze and compare the differences in benefits among wetland types.

- Develop valid methodologies for assessing each of these benefits in such a way as to make them additive.

- Test methodologies by applying them in various wetland circumstances (types, seasons, conditions) and by different researchers.

- Study the relationship between the number of wetlands in an area and the value of these wetlands per acre.

Impacts

- Conduct a comparison of watersheds to determine the amount (acres) and types of wetlands within each watershed. Select watersheds on both slopes of the Rockies, and at various latitudes from Canada to Mexico. Tabulate the numbers and types of impacts on wetlands and the extent of these impacts.

- In a large watershed region, compare the amounts of wetland being created with the amount of wetland loss due to human activities.

- Study the wetlands in Rocky Mountain "parks"--those intermountain basins--and compare the wetland in each with the nonwetlands in their vegetative structure, functional significance, and values.

- Conduct a study of the cumulative impacts on wetlands in the Rocky Mountains resulting from issuance of 404 permits. Are the wetland environment, structure, functions, and values equal to, better than, or less than before major and minor projects were allowed to develop?

- How productive and beneficial are wetlands created by mitigation procedures, by comparison with those destroyed? How do these factors vary with the technique used in mitigation, i.e., flood irrigation vs. lowering ground surface to just above the water table?

- What are the effects of streambank stabilization on adjacent riparian ecosystems?

- What is the minimal area of each wetland type that is needed to provide all the functions and values each gives the region?

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15. Supplementary Notes

16. Abstract (Limit: 200 words)

This ecological characterization of montane and subalpine wetlands encompasses the Rocky Mountain region from the Mexico border in New Mexico north to the Canada border in northern Montana and Idaho. The characterization has application to those wetlands located in adjoining mountainous regions of the Western United States. The document provides a general review of Rocky Mountain literature including discussion of geology, hydrology, climate, and soils. There is an especially comprehensive review of the ecological classification of montane and subalpine wetland communities with detailed descriptions of vegetation composition and illustration of many community types. Ecological processes, hydrologic relations, nutrient cycling, and productivity are also discussed. Multifunctional wetland values and impacts to wetlands resulting from developmental activities are described in considerable detail. The data contained in this report should assist scientists and managers throughout the Western United States in the wise development, management, and conservation of wetland resources in the Rocky Mountains.

17. Document Analysis a. Descriptors

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